FOREST Science

A QUARTERLY JOURNAL OF RESEARCH AND TECHNICAL PROGRESS

Volume 6-Number 3-September, 1960

PUBLISHED BY SOCIETY OF AMERICAN FORESTE

WASHINGTON, D. C

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Printed in the United States of America

FOREST *Science*

A Quarterly Journal of Research and Technical Progress

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Volume 6
September, 1960
Number 3

Some Effects of High Temperatures On the Cones and Seeds of Jack Pine

BY
WILLIAM R. BEAUFAIT

HISTORICALLY, fire has been the most important causative factor in the establishment of natural jack pine (*Pinus banksiana* Lamb.) reproduction. With today's rising demand for coniferous pulpwood, foresters are turning to prescribed fire in efforts to regenerate jack pine following harvest of mature stands. Before fire prescriptions could be made, however, it was necessary to clarify the effects of fire on the ripened cones and seeds of this species. Reported herein are the results from one of a series of studies designed to explore the behavior and aftermath of prescribed fire in the jack pine stands of northern Michigan.

The Jack Pine Cone

Jack pine is one of ten North American pines whose cones exhibit some measure of serotiny. Etymologically, the term "serotinous" derives from the Latin word *serus* meaning late. It is used in botanical literature to denote late appearing or late blossoming. Foresters refer to cones which do not open spontaneously after maturation as serotinous. Normally, cone scales separate and flex away from the cone axis soon after ripening. The seeds are thus freed for dispersion by wind and gravity. Cones which remain closed do so because of a resinous bonding material which seals the scales together and forms a vapor-resistant protective coating over the entire cone.

Temperatures exceeding those usually found in tree crowns are required for melting this resin and freeing the scales. Cameron (1953) found the melting point of the bonding material in jack pine cones to be about 122°F. This adaptation precludes a normal seeding pattern, seeds often being bound in serotinous cones for many years, even after the tree dies or is harvested.

Cone structure. The female jack pine cone consists of a central axis with bracts spirally arranged around it. In the axils of the bracts are potentially simple cones reduced to one sporophyll with two ovules (Gibbs 1950). For the purposes of this discussion the ovuliferous scales (megasporophylls or carpellate scales) will be referred to as cone scales. These structures are physical barriers to seed dispersion from a mature cone. The lower one-third or more of the jack pine cone does not produce seeds (Aase 1915), but these scales often restrict full opening of those above.

If the resin seal described above is melted, longitudinally oriented structures in the cone scale respond differentially to changes in moisture content. In a manner somewhat analogous to the action of the bimetallic element in a household thermostat, the individual cone scale curves away from the cone axis to liberate the seeds. The strongest curvature ocurs nearest the point of attachment to the cone axis, decreasing with proximity to the scale tip.

Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Michigan, Ann Arbor, Michigan. The author is now Research Forester, Ford Forestry Center, Michigan College of Mining and Technology, Houghton, Michigan. Manuscript received Dec. 2, 1959.

Variation in cone moisture content as it affects cone opening. Differential shrinkage of the scale tissues, as well as those of the attached bract, creates stresses inversely proportional to the moisture content of the atmosphere. This was demonstrated by glueing several cone scales to small blocks of wood in much the same fashion as they would be attached to a cone axis. After bringing the units to equilibrium in a saturated atmosphere, they were exposed to carefully controlled successively drier conditions ranging through 16, 12, 8, and 4 percent equivalent moisture contents (E.M.C.). In each case equilibrium was reached within a few days. All units exhibited a progressively increasing degree of curvature as moisture content decreased.

Of equal importance to the process of seed dispersal is the failure of excised scales to return to their original position when again subjected to a saturated atmosphere. After a scale has passed through a desiccating series, subsequent wetting and drying will result in less than full recovery. Eventually permanent deformation causes the scale to remain in a fully opened position regardless of its moisture content. The scale has been stressed beyond its elastic limit and "set" or plastic flow of the cellular material is likely to have occurred.

Cone moisture content in nature. The variation in moisture content of cones in nature is, therefore, important to seed dispersal. To assess this variation, 100 cones ranging in age from two months before ripening to about ten years after ripening were chosen at random from collections throughout northern Lower Michigan. Moisture content determinations were made on groups of three to four cones of like age with a reflux condenser and graduated trap. Age group determinations were based on color gradations to be described later. Commercial xylene (boiling point about 284°F) was used as the heat dispersal medium. After water extraction the cones were oven dried at 221°F for 24 hours to provide a base for comparison. All extractions were replicated.

The moisture content of full size green cones ranges between 250 and 350 percent of oven dry weight. This decreases rapidly with maturation to a level of about 12-15 percent when the cone has turned uniformly brown. Cones begin to show a greyish tinge on the weathered or exposed side within two years after maturity. About five years after ripening, cones remaining on the tree are light to dark grey in color on all sides. Color change is a reliable criterion for cone age. Over 100 whorl counts on live limbs from which cones were collected corroborated this color notation.

The mosture content of the oldest cones was consistently within two percent of that found for cones one year old. All were obviously at equilibrium with the atmosphere. These findings were essentially in agreement with moisture content determinations made by Ta Pa Ma in 1938 on jack pine cones from northern Minnesota (Schantz-Hansen 1941).

To test moisture content variation in nature further, dead twigs and open cones were broken from the limbs of standing jack pine trees in the vicinity of Afton, Michigan. No rain had fallen within a week prior to collection. Moisture contents were essentially the same for twigs three to six millimeters in diameter, the open cones, and adjacent closed cones.

In order to demonstrate an equilibrium of moisture content between cones and the atmosphere at other humidity levels, 50 additional samples were placed in controlled humidity chambers. These cones, which had reached a moisture content of seven percent in storage, were then placed in chambers maintained from four to 16 percent E.M.C. After six weeks, water extractions were made from the cones. In all cases cone moisture content was exactly the same as that of the E.M.C. of the chamber.

Low temperature desiccation of cones. Occasionally during the progress of this investigation, reports were heard of jack pine cones in nature opening after extended winter cold periods with temperatures well

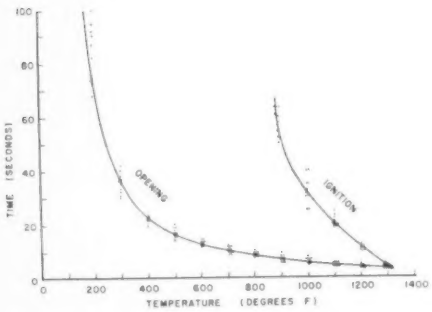

FIGURE 1. *Cone opening and ignition curves for cones at 8 percent moisture content (O.D.W. basis) in an open muffle furnace.*

below zero. Very low temperatures can cause moisture loss from biological materials through crystallization and subsequent sublimation of free water. To test the possibility of extreme cone desiccation and subsequent breakage of resin bonds under such conditions, three lots of three cones each were dried under vacuum at a temperature of minus 100°F. This process is called lyophilization or freeze-drying. A cone moisture content of 0.2 percent was achieved and maintained for three months. The resin bonds remained stable and no cones opened. Winter opening of cones must, therefore, involve phenomena other than desiccation alone.

With the foregoing evidence, it seems reasonable to assume that mature cone tissue does not receive moisture from the living portion of the plant but is in equilibrium with its environment. The resin coating on jack pine cones undoubtedly contributes to a time lag in moisture gain and loss but does not greatly affect the moisture content of cones in nature.

Cone Opening and Ignition

A basic consideration in attempts to regenerate jack pine with prescribed fire is the reaction of cones to high temperatures of varying duration. Commercial seed extraction procedures employing temperatures exceeding 140°F for several hours open cones with no measurable effect on seed viability. However, no published data concern time required for cone opening at very high temperatures.

To help to identify these parameters, 120 serotinous one- to two-year-old cones were selected at random from a collection representing all parts of the commercial range of jack pine in northern Lower Michigan. These cones were exposed one at a time to temperatures ranging from 200 to 1300°F in 100-degree intervals. Ten separate observations were made in an open muffle furnace at each temperature level. The time required for each cone to open was recorded in seconds. After opening, the cones were left in the furnace to furnish data on ignition time. Since cones exposed to temperatures of 800°F or less did not ignite within five minutes, ignition times are available only for the higher temperatures. Results of this test are presented in Figure 1.

The uniformity of results is remarkable considering the variation usually inherent in biological materials. At 400°F and above the cones opened within seconds of one another. The time required for ignition also varied only slightly for a particular time-temperature exposure.

The temperatures and durations illustrated in Figure 1 span those recorded in the crowns of seed trees during previously conducted prescribed burns. It might be expected that temperatures in a wild crown fire in the jack pine type would also fall within this range.

The Jack Pine Seed

Jack pine seeds are dark colored, are three to five millimeters in length and have loosely attached wings which facilitate their dissemination by wind. As with other pines, the seedcoat encloses oily megametophyte tissue of low water content (five to 20 percent) compared to wood or to the seeds of many hardwoods (Baldwin 1942; Gibbs 1950).

The hypocotyl and root cap elongate to crack the seed coat when temperatures and moisture conditions initiate growth. The cotyledons remain within the seed coat for

several days after germination. There are normally four to five cotyledons in jack pine seeds.

Normal viability. The average germination capacity of jack pine seeds in North America has been reported at about 68 percent (U. S. Forest Service 1948); however, to obtain some measure of normal viability in northern Lower Michigan, additional germination tests were made. Most tests were carried out on lots of 50 seeds placed for 30 days in a dark Mangelsdorf germinator adjusted to provide a daytime temperature of 80°F and a nighttime temperature of 68°F. Others were conducted at room temperature in flats containing moist sand with glass covers to prevent evaporation loss. In general, the sand flats indicated a higher germination capacity than did the commercial germinator for different lots of seeds from the same source.

A preliminary series of 35 tests was made for seeds from old, medium and young cones chosen at random from stands throughout the area. Results from these tests are summarized as follows:

Age of cones (years)	*No. tests*	*Mean total germination percentage*	*Standard error of the mean*
1-2	15	76	3.9
3-4	5	66	3.1
Over 5	15	33	9.1

Germination percentages of seeds from the older cones vary greatly, probably decreasing in proportion to their total age.

A separate series of 40 tests with 50 seeds each was made from one- and two-year-old cones collected near Higgins Lake and Afton, Michigan. The results were:

Seeds sown in:	*No. tests*	*Mean total germination percentage*	*Standard error of the mean*
Sand flats	20	80	1.8
Mangelsdorf germinator	20	69	2.8

Despite the superiority of sand flats for germination testing, the commercial germinator was used in the remaining tests for the sake of convenience and space economy.

Seed viability after exposure to high temperatures. If prescribed burning is to be useful as a silvicultural tool in the regeneration of jack pine, the seeds from serotinous cones must be released but not destroyed by the fire. Eyre (1938), for example, observed that cones in scattered slash were consumed by surface fires. What then is the condition of seeds dispersed from cones in the crowns of trees after a fire?

There are two possible results when scattered seed trees are surrounded by a hot slash fire. First, needles of the crown will ignite to produce a 40- to 60-foot torch, opening but rarely igniting the cones. Second, the crowns may not ignite but the cones will open due to heat radiated from the fire below. In a series of prescribed burns, it was observed that all cones on every seed tree could be opened by the heat of a heavy slash surface fire alone.

Seeds dispersed after the prescribed burns were not tested for viability. However, one- to two-year-old cones were exposed to a variety of high temperatures and durations in the laboratory. The seeds they contained were then collected and subjected to germination tests. To avoid sampling errors resulting from variation in the number of sound seeds per cone, germination capacity was computed after discarding the hollow seeds.

Starting with cones at room temperature, four lots of five cones each were exposed to 24 different time-temperature treatments in an open muffle furnace. Only actual cone ignition affected the viability of seeds. For example, the average total germination on five tests of cones exposed to 900°F for 30 seconds was 88 percent (standard error of the mean was 1.8) while those for 60 seconds had no viable seeds remaining.

To test the limit of viability below 800°F, cones were exposed to 700°F for one-, two-, and three-minute intervals. Viability did not fall off significantly until the three-minute exposure. No seeds survived this last treatment and the cones were

ashed to the point of crumbling under slight pressure.

Since the heat liberated by either surface fires or crown torching does not ash the cones of standing trees and since very high temperatures are not likely to last as long as three minutes in the crowns of seed trees, it is logical to conclude that seed viability is not markedly affected by prescribed burning.

To test the above conclusions further, seeds unprotected by cone scales were subjected to temperatures up to 1000°F. These seeds were extracted at 140°F over a period of 12 hours (a normal extraction schedule) from one- to two-year-old randomly chosen cones. Wings were not removed from the seeds. Lots of approximately 50 seeds were exposed to high temperatures ranging from 700°F to 1000°F for periods up to 20 seconds. Not until the wings ashed and the seed coats cracked from internal pressure did viability decrease significantly. The time periods during which this damage occurred are:

Degrees F	*Seconds*
700	10 to 15
800	5 to 10
900	0 to 5
1000	0 to 5

These data suggest that jack pine seeds are very heat resistant and that the cones themselves provide considerable protective insulation. Even when the cone scales separate slightly with volatization of the resin seal, the physical barrier to radiation posed by the scale, coupled with the probable vaporization of cone moisture, prevents seed destruction.

Summary and Conclusions

The process by which mature serotinous cones of jack pine open to disperse their seeds has been described, note being made of the need for temperatures exceeding 140°F to break resinous bonds on cone scales. The function of structural variation in the cone as a cause of reflection of the individual scale has been discussed.

Tests were conducted which show the dependence of cone opening on ambient atmospheric humidity. Cone moisture content was found to vary in nature from 350 percent of oven dry weight when green to 7 percent when mature. Mature cones were found to be at equilibrium with atmospheric moisture. Further desiccation of cones at extremely low temperatures was achieved under laboratory conditions, but the stresses incurred failed to break resinous seals on the cone scales.

Cones taken from a collection representing serotinuous trees in all parts of northern Lower Michigan were exposed to temperatures ranging from 200°F in 100-degree intervals for periods up to five minutes. They responded consistently by opening in a range from 80 seconds at 200°F to two seconds at 1300°F. The cones ignited in 60 seconds at 700°F; in only two seconds at 1300°F. Cones which ignited retained no viable seeds while unignited cones suffered but little reduction in the germinative capacity of their seeds.

Normally extracted jack pine seeds were also exposed to high temperatures and demonstrated an ability to remain viable until the wings ashed and the seed coats cracked from the heat. At 700°F this occurred between 10 and 15 seconds' exposure; at 1000°F, between 0 and 5 seconds.

The results suggest that the high temperatures incurred in the crowns of standing trees during prescribed burns will not impair the viability of the seeds in serotinous cones, but should aid their dispersion.

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Physiology of Trees

By Paul J. Kramer and Theodore T. Kozlowski. McGraw-Hill Co., Inc., New York, 642 pp., illus. 1960. $12.50.

Review by Henry Hellmers
Pacific Southwest Forest and Range Experiment Station
Forest Service, U. S. Department of Agriculture

How often have you asked, "How Does A Tree Grow?" In this book Kramer and Kozlowski have done an excellent job in assembling and interpreting the available information on this subject. The answer to the question has many ramifications including "ifs, ands, and buts." In areas where controversy exists they have carefully presented both sides. Furthermore, they have pointed out areas where information is inadequate or entirely lacking, and there are many such areas in this young, rapidly growing, field of tree physiology.

The ecological approach to tree physiology is stressed throughout the book, which makes for interesting and easy reading even for one not specifically trained in physiology. The ecological approach has been taken at the expense of detailed biochemical and biophysical explanations of the physiological processes. My one criticism would be that the book might possibly have been better titled "Physiological Ecology" or some similar name, as more descriptive of its contents. However, for those interested in more details on the biochemical and biophysical aspects, the book is extensively and exceptionally well documented. The text contains citations to more than 1600 references listed in the bibliography and there is a short list of general references at the end of each chapter.

The organization of the book is such that it can be used readily as a text or reference. For those less familiar with the subject the book starts with a description of tree structure and growth in terms of meristems and organs. The chapters that follow deal with the physiological processes that occur within a tree, including photosynthesis, metabolism and end products, respiration, transpiration, mineral nutrition, and translocation of water, organic compounds and minerals. Information on seed physiology and germination is assembled in a separate chapter. The last chapter discusses the environmental factors and their effect upon tree growth. The entire book is well illustrated with photographs, graphs, and diagrams to emphasize and demonstrate the points being presented. The numerous chapter subsections along with the many citations add greatly to the value of the book as a reference source.

To biologists and especially foresters this book fills a definite need for a compilation and interpretation of the latest information on tree physiology and its relation to tree growth. As a text book it furnishes a broad foundation for further study in the specific phases of plant physiology or ecology. As a reference book for anyone interested in growing trees it provides an excellent review source with an extensive bibliography.

Ecotypic Variation of Photoperiodic Response in Trees Especially in Two Populus Species

BY
O. VAARTAJA

TREES of a northern climate are especially adapted to survive the cold season. The yearly alternation of active growth and dormancy is obviously an important mechanism in this adaptation. Surprisingly it has been found that daylength is one of the environmental factors which may control the alternation. Since daylength of the warm season in general is long in high latitudes and short in low latitudes, it is to be expected that northern and southern trees have evolved with different responses to photoperiods. As far as such different evolutions have taken place within a species, the northern and southern populations may be considered as different ecotypes.

The existence of photoperiodic ecotypes in trees was first indicated by Sylven (1940) for seedlings of *Populus tremula* L. (see also Grehn, 1952). It was then established for cuttings of *P. trichocarpa* Torr. & Gray by Pauley and Perry (1954) and for seedlings of *Pinus silvestris* L. and *Alnus incana* (L.) Moench by Vaartaja (1954a). The data of Pauley and Perry (1954) suggest that there are photoperiodic ecotypes also in *P. balsamifera* L. and in *P. deltoides* Bartr. Recently, significant photoperiodic differences have been found between northern and southern seedlings in 16 of about 18 more tree species properly tested so far (Downs and Piringer, 1958; Vaartaja, 1959).

In the following a test is reported for possible photoperiodic differences between northern and southern seedlings of cottonwood (*P. deltoides*) and quaking aspen (*P. tremuloides* Michx.).

Methods

Seeds from the following low elevation sources[1] were utilized:

Populus deltoides: St. Paul, Minn., U. S. A., North Lat. 45° and Baton Rouge, Louisiana, U. S. A., North Lat. 30°.

Populus tremuloides: Prince Albert, Sask., Canada, North Lat. 54° and Eagle River, Wis., U. S. A., North Lat. 46°.

Seeds were sown in glass jars in a mixture of sand, sphagnum moss, and forest humus. One to four seedlings were grown in each jar.

The jars were kept in growth rooms under 4 x 4 ft light banks with 12 cool white fluorescent tubes and 4 tubular 25 W incandescent bulbs. The light intensity varied between 400 and 800 foot candles at the tips of the plants depending on the height of these. The temperature varied

[1]Seed was obtained through the courtesy of Charles B. Briscoe, Louisiana, and Paul O. Rudolf, Minnesota.

Contribution No. 590, Forest Biology Division, Research Branch, Canada Agriculture, Ottawa, and No. 32, Canada Agriculture Research Station, Saskatoon, Sask. The author is attached to the Forest Biology Laboratory, Saskatoon, Sask. Manuscript received Nov. 6, 1959.

from 60°F. at night to 80° (sometimes 70° or 90°)F. during the day. The photoperiodic treatments were arranged as shown in Figure 1. "Long day" treatments were approached by giving supplementary light for one hour once or 3 times at different times during the night. It is well known that the photoperiodic responses depend mainly on the maximum length of the uninterrupted dark periods rather than on the total length of daily light or dark periods. The extremely short day (ESD) treatment was not given to the aspen.

Tests with cottonwood and aspen were conducted separately. In each, the northern and southern seedlings were arranged in pairs, each replicated 8 to 11 times. The seedlings of all origins generally grew larger under long than short photoperiods. This response is well known and will not be described in this paper. Instead, the variation in this response for seedlings of different origins was investigated. In other words, the interaction of treatments and the origins was studied. To get a most direct and valid measure of this, the growth data were calculated as ratios N/S. This means, for instance, that if a northern (N) seedling grew 20 mm high and its southern (S) pair 40 mm, a N/S ratio of 0.50 was recorded for height. The ratio data showed much more variation under certain treatments than under others. Therefore, analyses of variance were conducted separately for each two of related treatments (ELD vs. LD, LD vs. SD, SD vs. VSD, and VSD vs. ESD).

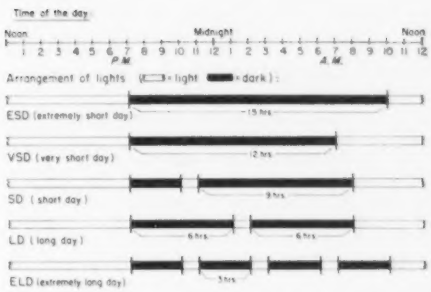

FIGURE 1. *Arrangement of daylength treatments by means of light breaks during the dark period.*

Results

The main results, as recorded when the seedlings were about 6 months old, are shown in Tables 1 and 2.

Short-day treatment (SD) inhibited the growth of Saskatchewan seedlings of aspen drastically. Most of these formed terminal buds early and ceased elongating. This resulted in very low N/S ratios as most of the Wisconsin seedlings continued elongating. Under LD few northern seedlings were inhibited, and these only slightly. This inhibition was expressed mainly in the

TABLE 1. Interaction of seed source and photoperiod in the growth of aspen. Ratios (N/S) of Saskatchewan and Wisconsin seedlings under different daylength treatments.[1]

Expression of growth	Ratio N/S under VSD		SD		LD		ELD
Length of stem	.4***	>	.2		.5*	<	1.0
Total dry weight	.5**	>	.2*	<	1.3		1.2
Weight of stem only	.5		.2*	<	1.1		1.1
Weight of top	.3**	>	.05*	<	.9		1.1
Weight of roots	2.4*	>	.6*	<	4.3		2.9
No. of leaves	.8**	>	.4**	<	.6**	<	1.0

[1]The asterisks indicate that the value was different from the value at right; P levels: *** 0.1%, ** 1%, * 5%, the marker > points towards the smaller of 2 values.

length of stem and in the number of leaves.

Under VSD the ratios were higher than under SD because both the Saskatchewan and Wisconsin seedlings were inhibited by VSD. Under ELD all the seedlings continued growing well throughout the test.

The Saskatchewan seedlings had much heavier roots than the Wisconsin seedlings under VLD, LD and even under VSD; only under SD was the ratio below 1.0 as the northern seedlings were inhibited but the southern ones not. Even here the root ratio was higher than the ratios of other growth expressions. Perhaps the heavier roots of the northern seedlings were a genetic adaptation to the colder soils. The balanced function of roots and top may require large root systems in northern soils, which are known to be very cold. The low temperature and the lag in warming in northern soils is a result of the short summer and of the insulating effect of the typically thick humus and litter covers (Vaartaja, 1954b). Similarly it has been found that the roots were relatively heavy in *Betula papyrifera* Marsh. from an extremely far northern site (Vaartaja, 1959) and in *Pseudotsuga menziesii* (Mirb.) Franco from high altitudes (Owen, 1958).

The cottonwood from Minnesota generally grew somewhat larger than that from Louisiana (Table 2). This was attributed to the fact that the Minnesota seeds happened to be larger and germinated earlier. Nevertheless most of the N/S ratios were below 1.0 under VSD as this was inhibitory to Minnesota seedlings. The Louisiana seedlings were inhibited by ESD. The inhibited seedlings of both sources soon formed terminal buds.

It is interesting to note the longest inhibitory ("critical") daylengths for the seedlings from different latitudes:

Species	*Lat.*	*Inhibitory treatment*	*Corresponding (longest) dark period*
Aspen	54°	SD (partly LD)	9 (6) hrs.
Aspen	46°	VSD (partly SD)	12 (9) hrs.
Cottonwood	45°	VSD	12 hrs.
Cottonwood	30°	ESD	15 hrs.

This shows a correlation of the length of the critical photoperiod with the latitude of the seed source. The earlier data (Vaartaja, 1959) on several species of various genera showed similar correlations, especially in comparisons of closely related trees.

The critical daylengths and dark periods shown above correspond, at least roughly, to the daylengths and nights at the time of the year generally becoming too cold for growth. The data are therefore consistent with a hypothesis according to which the photoperiodic ecotypes of aspen and cottonwood have evolved as mechanisms for full utilization of the warm season and for

TABLE 2. Interaction of seed source and photoperiod in the growth of cottonwood. Ratios (N/S) of Minnesota and Louisiana seedlings under different daylength treatments.[1]

Expression of growth	Ratio[2] N/S under ESD[3]		VSD		SD	LD
Length of stem	1.4***	>	.5***	<	2.0	1.8
Total dry weight	1.2***	>	.5***	<	1.6	2.2
Weight of stem only	1.0**	>	.5***	<	3.0	2.1
Weight of top	1.0***	>	.3***	<	1.5	1.3
Weight of roots	1.6		1.1*	<	1.9	2.0
No. of leaves	1.2***	>	.8**	<	1.3	1.4

[1]The asterisks indicate that the value was different from the value at right; P levels: *** 0.1%, ** 1%, * 5%; the marker > points towards the smaller of 2 values.

[2]Minnesota seedlings were favored by larger seeds and earlier germination.

[3]Kept at first under ELD, later under ESD; under ELD the seedlings grew in about the same manner as under LD

preparation against early frosts and winter cold. The trees with unsuitable photoperiodic responses would be seriously unadapted. A tree inhibited by longer photoperiods than the population in general would become dormant while the season still is warm.

A tree inhibited by shorter photoperiods, would not be dormant and hardy when the cold season begins. (This has been actually found when trees have been transferred to photoperiods longer than on their native sites; Moshkov, 1935; Sylven, 1940; Schulz, 1949; Pauley and Perry, 1954; further discussion by Vaartaja, 1954a and 1959). In either case such trees would be eliminated in the competition with the rest of the population. The result thus would be a selection for, and an evolution of such photoperiodic ecotypes as were actually found and which have a favorable timing of dormancy.

Discussion

The results with seedlings of cottonwood (Table 2) agree with the results of Pauley and Perry (1954) concerning the photoperiodic variation in cottonwood cuttings, and indicate the existence of photoperiodic ecotypes in this species. Similarly the existence of photoperiodic ecotypes was indicated in *P. tremuloides* (Table 1). This is in accordance with the findings of Sylven (1940) and Grehn (1952) on the closely related *P. tremula*. The variation in photoperiodic responses was similar to that found in most other genera of trees (Vaartaja, 1959) and to what would be expected according to the hypothesis of photoperiodic ecotypes.

To show the interaction in a most illuminating way, seedlings from the cottonwood test were selected to represent the effects of two contrasting ecotypes and photoperiods. Photographs of these are shown in Figure 2. This demonstrates that both the genetic and environmental factors need to be considered when discussing factors determining the growth of trees. Although an extensive provenance trial may suggest a tree race as inferior or superior to others, it may be so only in a certain area. More extensive trials than exist now are needed to get a reasonable idea of the potentialities of any tree race or ecotype. Increased coordination through international cooperation is necessary to accomplish this.

The characteristically slow growth of northern trees in trials located far south may be mainly caused by the unsatisfied requirement for long days. This was suggested, for instance, by the results of an international trial series with *Picea abies* (L.) Karst. (data of Heikinheimo, 1954; elaborated by Vaartaja, 1959). The results concerned growth of seedlings of 11 origins from Lat. 42° to 66° in 5 nurseries located from Lat. 47° to 66°. Contrasting parts of the results are shown in Figure 3.

If the photoperiod were an important factor governing growth under natural, non-optimal conditions, great differences would be expected between trees transferred far south from their origin (to a critically short daylength) and the other trees in each trial. This was the case in *P. abies* as illustrated in Figure 3 by the low growth values of the northern provenances in the southern (51°) test.

On the other hand, the differences between other trees within each trial would be expected to be relatively small. This again was the case as shown by the similarity of each value in the northern test (66°) and of each value of the different southern provenances in the southern test. In the northern test the northern trees grew less than the southern ones; they supposedly possessed a safety margin against abnormally early cold and became dormant (as a response to daylength of a certain date) when cold does not normally occur. As a result of too long seasonal growth the southern trees were damaged during some of the subsequent autumns in the north.

This example and the results of many other provenance trials (discussed by Sylven, 1950; Vaartaja, 1954a, 1959; Langlet, 1959) suggest that photoperiodic responses determine the growth of trees to a large extent. An understanding of photoperiodism should become recognized as a necessity

in forest science.

The discussion above considers only the differences between northern and southern populations. As the photoperiodic response and its variation likely function and have evolved as an indirect adaptation of trees to factors other than photoperiod itself, the responses should not be expected to be the

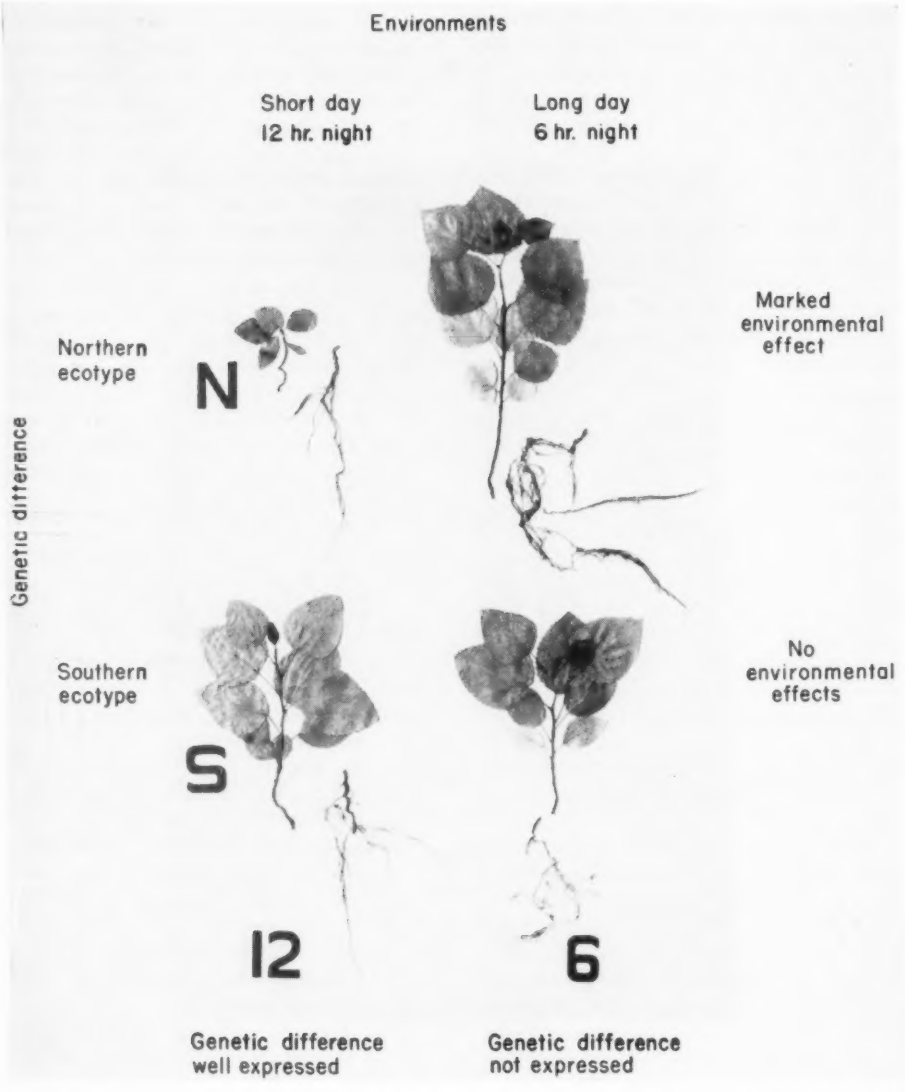

FIGURE 2. *Interaction of daylength and seed source in the growth of cottonwood from Minnesota (N), and from Louisiana (S). (Treatments described in Figure 1.)*

same everywhere in each latitude. There is in fact evidence that the photoperiodic response generally varies with altitude (Karschon, 1949; Pauley and Perry, 1954; Irgens-Moller, 1958; Owen, 1958) and with the continentality of the climate (Owen, 1958; Vaartaja, 1959).

Fully or partly dormant trees obviously can be more resistant to drought than actively growing trees. On critically dry sites natural selection may therefore favor ecotypes that become partially dormant regardless of the photoperiod or as a response to the photoperiods of midsummer, long before the cold season starts. It is plausible that in certain trees, e.g., in pines, ecotypes have evolved in this way (Vaartaja, 1959).

The results in Tables 1 and 2 indicate that in each ecotype a certain daylength was critical to various growth expressions. However, the elongation of some of the aspen seedlings was partially inhibited by longer daylength than which inhibited weight increases and development of leaves. This tendency is much more obvious and greater in certain other tree species (Vaartaja, 1959). A way of elongating in short flushes even under long days may have evolved because of the reduced risk to the sensitive and important apical part of trees. In northern trees the potential second flush may be inhibited by a daylength that still allows growth in other parts of trees.

The discussion above ignores factors other than photoperiod. This is done to simplify the presentation of the main theme and because in the experiments the effects of other factors were minimized by simulating or approaching optimum conditions. In nature, however, the photoperiodic response in trees is likely masked and modified by many factors, especially by temperature (Moshkov, 1935; Wareing and Black, 1958; Downs and Piringer, 1958; Waxman, 1958).

Differences in response to photoperiods are not the only important differences between latitudinally distant populations (Wang and Perry, 1957; Perry and Wang, 1957; Langlet, 1959; Vaartaja, 1959). It is to be expected that the responses to various ecological factors are different in populations of different environments. To avoid confusion the following suggestion is made for future terminology. A term such as "edaphic ecotype" or "temperature ecotype" should be used when considering differences in responses to a certain factor (even when it happens to coincide geographically with photoperiodic or other ecotypes). Terms such as "maritime ecotype" or "northern ecotype" should be used when considering several or all the ecological responses of a population. These genecological terms should not be considered synonymous or analogous with the taxonomic ones. For instance, the ecological groups are usually separated by gradual variation (see convincing data and a discussion by Langlet, 1959) while the taxonomic groups are, or at least should be, separated by a discontinuity.

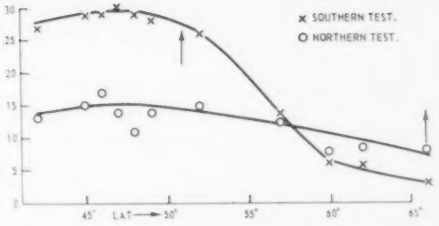

FIGURE 3. *Growth (total fresh weight of 200 seedlings in grams) of* Picea abies *seedlings from 11 different latitudes in two tests in two widely distant latitudes. Arrow points to the curve and latitude of each test. (Data from Heinkinheimo, 1954.)*

Summary

The photoperiodic responses of seedlings of *Populus deltoides* and *P. tremuloides* from northern and southern origins were tested experimentally. The northern seedlings were inhibited by longer days than the southern seedlings. This interaction of photoperiod and origin was expressed in stem length, total dry weight, dry weight

of stem without leaves, dry weight of tops with leaves, dry weight of roots, and number of leaves.

The longest inhibitory ("critical") daylength was correlated with the latitude of the seed source. It is suggested that the photoperiodic response and ecotypes in these species have evolved in the populations of latitudinally distant sites as an indirect mechanism in utilization of the warm season and in preparation against the cold season.

The weight of the root systems was found to be much greater in Saskatchewan aspen than in Wisconsin aspen (except under the critical daylength that inhibited Saskatchewan seedlings but not those from Wisconsin). This appears to be a genetic adaptation to the cold soils in the north.

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Stimulation of Cone and Seed Production In Pole-Size Loblolly Pine

BY
M. VICTOR BILAN

INTENSIVE FORESTRY and short rotations practiced by pulpwood growers require prompt regeneration of forest stands, which, in turn, depends to a great extent on an adequate and dependable seed supply. Large fluctuations in annual seed production of forest trees, therefore, present a serious problem.

Certainty of adequate seed production is particularly important in the southeastern United States. Here conditions favorable to seed germination and seedling establishment of southern pines deteriorate rapidly after cutting because of hardwood sprouting and increase of herbaceous vegetation. In this region seed supply often is insufficient because many pine stands are harvested for pulpwood when of pole size, and the remaining trees often are too young to produce enough seed for natural regeneration.

It is widely believed that seed production can be increased by girdling or strangulation of the stems as well as by exposure of the crowns to full sunlight. Girdling and strangulation are the oldest and most popular methods practiced by horticulturists, whereas crown release has been the only common practice used to stimulate fruitfulness in forest trees.

Girdling may consist of one continuous incision around the stem or two overlapping semi-circular incisions with a vertical separation of one to a few inches. Strangulation is carried out by winding a soft iron wire or a metal band tightly around the stem. As the diameter of the treated stem increases, the phloem becomes more and more constricted, and the downward flow of assimilates is inhibited. Both girdling and strangulation result in accumulation of carbohydrates above the point of treatment, thus stimulating flower-bud initiation and fruiting.

Unlike orchard trees, forest trees often grow under crowded conditions, and release of crowns from competition usually has a pronounced effect on seed production. Crown release was familiar to early European foresters, who often made preparatory cuttings prior to the final harvest and natural regeneration of forest stands. Such preparatory cuttings were really preharvest crown releases, which improved light conditions in residual stands and resulted in prolific seed production.

Under the direction of Professor C. F. Korstian, an experiment was initiated in the Duke Forest in 1952 to determine the effectiveness of several methods of stimulating cone and seed production of pulpwood-size loblolly pine (*Pinus taeda* L.). This paper deals with the analysis of data

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Part of dissertation submitted in partial fulfillment of the requirements for the D.F. degree in the School of Forestry, Duke University, Durham, North Carolina.

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Acknowledgement is due to K. L. Carvell for painstaking work in the establishment of the experiment, and to H. W. Hocker, who assisted in collecting the data.

collected during five years of experimentation and with physiological and silvicultural interpretation of the results.

Review of Literature

The fruiting of a tree involves several proceseses such as the formation of flower buds, blossoming, fertilization, seed development, and seed ripening. Each process can be profoundly affected by age, crown development and heredity of a tree as well as by the biotic and physical factors of its environment. Flower-bud formation alone, for example, is governed by such biotic factors of the plant as age, morphological development, inherited fecundity, correlation between vegetative and reproductive growth, and by environmental factors such as soil and weather.

The study of seed production of loblolly pine is made more difficult by the fact that the developmental cycle requires three growing seasons. Flower buds, young cones, and maturing cones are found on the same tree, and frequently even on the same twig. This overlapping of three periods of sexual reproduction and their superimposition on annual growth cycles complicates the study of nutrient requirements and the metabolism of fruiting.

The earliest known attempt to stimulate seed production in forest trees by horticultural methods was made by Busse (1924) in Germany. He claimed that, by breaking off the tips of young shoots in 19-year-old Scotch pine (*Pinus sylvestris* L.) in early spring, he was able to increase flower bud production for three consecutive years. However, most of the work dealing with stimulation of fruiting in forest trees has been done during the last two decades.

Stimulation of fruiting in forest trees by girdling and strangulation was reported by Pond (1936), Jensen (1942, 1943), Arnborg (1946), Stefansson (1948), Holmes and Matthews (1951), Wenger (1953), and others. Bergman (1955) and Hoekstra and Mergen (1957) reported an increased production of female flowers in pine as a result of strangulation and girdling in combination with root pruning and/or fertilization. Most investigators agree that increased flower production is evident two to three years after the treatment.

Failure of girdling and strangulation to stimulate seed production in spruce and pine was reported by Vincent (1940) and Girgidow (1956). Girgidow also stated that glucose injection and root and crown pruning failed to increase seed production.

The Forestry Research Institute in Moscow[1] reached the following conclusions after 20 years of experimentation on stimulation of seed production in forest trees. Girdling, bark ringing, wiring, and banding decreased vigor of trees and resulted in the death of most treated trees in 4 to 6 years following treatment. Crown and root pruning decreased fruiting of experimental trees, and 4 to 5 years were required for seed production of treated trees to catch up with that of control trees. Exposure of entire crowns to full sunlight gave the best results. During 20 years, released trees produced 6 to 8 times as much seed as did unreleased trees. The trees in released stands began to bear seed when they reached an average d.b.h. of 3 inches, while trees in unreleased stands did not bear seeds until they were at least 6.3 inches.

The effect of full crown release on seed production of forest trees has been observed and studied by many workers in this country and abroad. Because of the extensive literature, this review will be limited to studies dealing mainly with crown release in loblolly pine.

Chapman (1923) and Forbes (1939) observed that residual loblolly pines on cut-over areas produced more cones than did trees in uncut stands. Shelterwood cutting (Pomeroy and Korstian, 1949) and alternate strip cutting (Trousdell, 1950) resulted in increased seed produtcion of residual pines. Positive effect of crown release on seed production in loblolly pine was reported by Wenger (1954), Easley

[1]Personal correspondence, December 1956.

(1954), and others. Many studies show that the stimulating effect was noticed in the first flower-bud formation following crown release and it continued for several years.

Field Experimentation

Site Conditions

The experimental area was located in the Duke Forest, Durham, North Carolina. The predominant soil type was Appling sandy loam with 14 to 34 inches of topsoil underlain by a friable sandy clay subsoil. The site index for loblolly pine was 85 feet, an excellent upland site.

The average annual precipitation in the vicinity, based on a 25-year record, is 42.5 inches, with the maximum in July and the minimum in November. Droughts may occur any time between March and October (U. S. Weather Bureau, 1929-54).

Although the average annual temperature is about 51°F, extremes of −10°F and 107°F have been recorded. The temperature reaches the maximum in July and the minimum in January. The average length of the frost-free season is approximately 200 days.

The experimental stand was planted in 1932 with a 7- by 7-foot spacing. It was given a crown thinning in 1948 when 5 cords of pulpwood were removed per acre. The trees were 21 years old when the experiment was initiated in the early spring of 1952.

Design and Establishment of the Experiment

On an area of about 50 acres, 220 dominant loblolly pines were selected and numbered consecutively. On one half of the experimental area crowns of 110 selected trees were exposed to full sunlight by removing all other trees whose crowns were within 6 feet. The remaining 110 selected trees were allowed to grow in a closed stand.

The experimental trees were divided into 44 blocks of 5 trees each. Within each block one tree was used for each of the three treatments and two untreated trees were selected at random as controls. Thus each block consisted of one partially-girdled, one wired, one banded, and two control trees. All treatments were imposed on the tree trunks 6 feet above the ground during the first two weeks in April, 1952.

Partial girdling consisted of two semicircular incisions completely encircling the stem with ½-inch overlap and two inches apart vertically. The incisions were made with a timber scribe by cutting through the phloem to the outer xylem. Wiring treatment consisted of wrapping a stem with 14-gauge galvanized steel wire. Two double strands of wire, approximately 1.5 inches apart, were tightened around the stem with pliers and a piece of iron rod. For the banding treatment an aluminum band $\frac{1}{16}$ inch thick and 1.5 inches wide was wrapped around the stem. The ends of the band overlapped 2 to 4 inches. The band was then fixed tightly in place by a double strand of 14-gauge galvanized steel wire. The trunks of control trees were left undisturbed.[2] Before the wires and bands were applied the rough outer bark of each stem was shaved until only a thin layer of bark remained at the points of treatment.

The experiment was set up to be analyzed as two sets of randomized blocks, one containing released trees and the other the unreleased trees. The double number of control trees, as compared with trees in any other treatment, was intended to provide a strong test for the effect of the treatments.

Effects of Treatments on Cone and Seed Production

Methods

Cone counts were made with binoculars in the spring of 1952 (crop of 1951) and in autumns of 1952, 1953, and 1954. Counts were made simultaneously and independently by two ground observers, who moved around the trees and attempted to count all visible cones. Averages of these two re-

[2]The wires and bands were removed in the winters of 1954-55 and 1955-56, respectively.

corded counts were used in analysis of data. In 1954, 1955, and 1956, trees were climbed with a ladder and cones were then counted.

During the counting period in 1955 cone samples were collected from each bearing tree to determine the number of viable seeds per cone. Samples were selected from a branch in the third whorl from the tip on the northwest side of the crown. When the corresponding branches in the third whorl were barren, a sample was collected from the second whorl from the tip. When cones were borne on branches below the fourth whorl from the tip, a second cone sample was collected from the lowest bearing branch on the northwest side of the crown.

Care was taken to collect cone samples from the same exposure and same position on the crown because it had been shown by Acatay (1938) that in Scotch pine the number of viable seeds per cone changed with exposure and position of cones in the crown.

After storage of cone samples at room temperature for two months, the seeds were extracted and their viability determined by cutting. Seeds which contained white endosperm were considered to be viable.

Results

Cone production, 1954-55. Average annual cone production per tree during the period of experimentation is presented in Figure 1. Only the summation of data for 1954 and 1955 was subjected to analysis of variance because the crop of 1953 was a total failure due to a late freeze in the spring of 1955.

Full crown release of 21-year-old pines considerably increased cone production during the third and fourth growing seasons following the treatments. In 1954 and 1955 average cone production per tree was 93 for the released and 20 for the unreleased trees.

Although the number of cones produced per tree in the released portion of the stand during the period 1954-1955 was highest

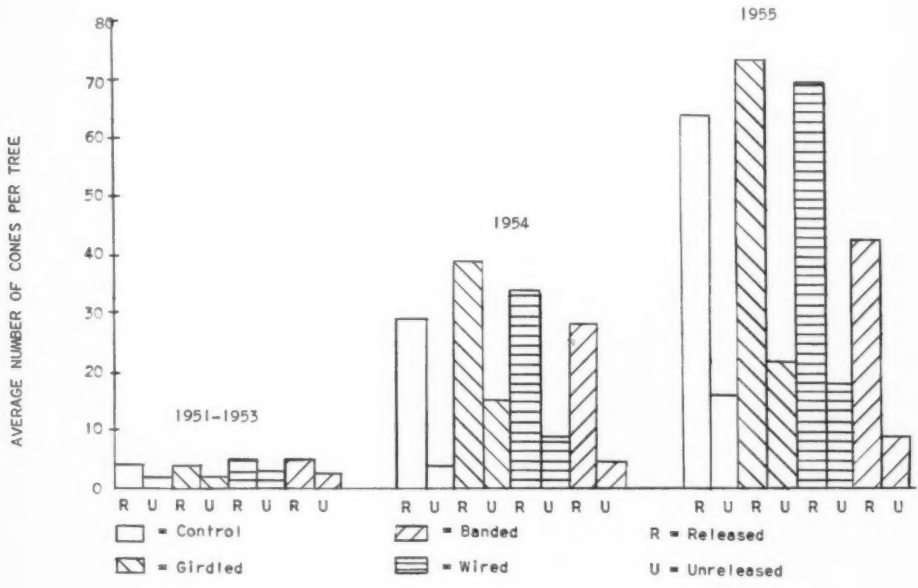

FIGURE 1. *Average annual cone production per tree in 1951-1955.*

for the girdled trees and successively less for the wired, control, and banded trees, the differences were not statistically significant.

Cone production of treated trees in the unreleased portion of the stand followed the general pattern of the released trees but the number of cones produced was much lower. In this instance, however, the decreased production by the banded trees was more conspicuous; the difference between the banded and control trees as well as between the banded and girdled trees was significant at the 5-percent level.

Viable seeds per cone. Full crown release increased the number of viable seeds per cone by 67 percent (Table 1). While the girdled, wired, and control trees in the released stand produced 46, 47, and 45 viable seeds per cone, respectively, the banded trees bore only 24 viable seeds per cone, a 50 percent reduction. This difference was significant at the 1-percent level.

In the unreleased portion of the stand the control trees produced an average of 27 viable seeds per cone, while the trees in each of the three remaining treatments bore an average of only 19 viable seeds per cone. The difference was significant at the 10-percent level.

The number of viable seeds per cone borne on the third whorl from the tip or above was consistently at least 30 percent higher than the number of viable seeds per cone borne on the branches below the fourth whorl from the tip. This relationship was constant for all treatments in the released portion of the stand. The difference was statistically significant at the 1-percent level. It could not be determined if a similar relationship existed in the unreleased part of the stand, because most unreleaseed trees bore cones only at the crown tips.

For the cone crop of 1955 no significant correlation existed between the number of cones per tree and the number of viable seeds per cone. This relationship held for both the released and unreleased portions of the stand.

TABLE 1. Average number of viable seeds per cone in 1955.

Treatment	Released trees		Unreleased trees	
	Mean	Standard error	Mean	Standard error
	Seeds			
Girdled	46.0	±5.5	19.1	±5.0
Wired	47.4	±6.0	19.2	±4.8
Banded	24.2	±5.7	19.4	±5.2
Control	44.5	±4.0	26.6	±3.3

Number of viable seeds per cone-bearing tree. Only 80 percent of unreleased trees bore cones in 1955 as compared with 100 percent for released trees. The average released, cone-bearing tree produced six times as many viable seeds as the average unreleased bearing tree (Table 2). Although banded, released trees did not lag in cone production, they did so in seed production due to a low number of viable seeds per cone.

In the unreleased portion of the stand girdled trees produced the highest number of viable seeds while banded trees bore the fewest. These differences were not statistically significant due to a very high variation in the number of cones per tree and the number of viable seeds per cone.

TABLE 2. Average number of viable seeds per cone-bearing tree in 1955.

Treatment	Released trees		Unreleased trees	
	Mean	Standard error	Mean	Standard error
	Seeds			
Girdled	3,531	± 857	1,101[2]	± 371
Wired	3,976	± 925	690	± 358
Banded	1,426[1]	± 878	384	± 384
Control	3,396	± 621	559	± 245

[1]Significantly lower than any other treatment.
[2]No significant difference among the treatment means.

Effect of Treatments on Tree Growth, 1952-1956

Total height, d.b.h., crown length, and crown width of each experimental tree were recorded at the beginning of the experiment in 1952 and at its termination in the autumn of 1956. The 1952-data are summarized in Table 3, while the changes during 1952-1956, adjusted for the differences existing in 1952, are presented in Table 4.

During six years of study, the average released tree grew in d.b.h. 1.9 inches as compared with 1.4 inches for the average unreleased tree. Significant reductions in diameter growth were caused by girdling and wiring unreleased trees. No other treatments affected diameter growth significantly. It is believed that in 1952, and probably in 1953 also, diameter growth of released girdled and wired trees was below that of released control trees, but by 1956 these differences were offset by the high rate of growth in the released portion of the experimental stand.

Height growth from 1952 to 1956 amounted to 6.0 feet and 7.8 feet for released and unreleased trees, respectively. Neither girdling nor strangulation affected height growth of released or unreleased trees.

In the spring of 1952 the average live-crown ratio was 44 percent for the released

TABLE 3. Average total height, diameter at breast height, crown ratio, and lateral crown area of experimental trees at the beginning of the experiment in 1952.

Treatment	Total height in feet	D.b.h. in inches	Live-crown ratio	Lateral crown area in square feet
Girdled				
Released	56	10.3	44	201
Unreleased	56	9.9	43	227
Wired				
Released	54	9.5	44	198
Unreleased	57	9.8	43	240
Banded				
Released	55	9.9	46	200
Unreleased	56	9.5	43	232
Control				
Released	54	9.5	44	195
Unreleased	56	9.6	42	219

TABLE 4. Summary of average growth and development of the experimental trees during the period 1952-1956.

Treatment	Released trees				Unreleased trees			
	Control	Girdled	Wired	Banded	Control	Girdled	Wired	Banded
Height growth (feet)	5.6	6.3	5.4	5.9	8.4	7.9	7.4	8.0
D.b.h. growth (inches)	1.91	1.93	1.74	1.96	1.41	−1.11**	1.22*	1.48
Change in percentage of live-crown ratio	+2.9	+5.3*	+5.0*	+4.3	−5.3	−4.4	−7.5*	−6.6
Change in lateral crown area (square feet)	+129	+150	+121	+127	−16	−19	−48**	−28

**Difference from control significant at the 1-percent level.
*Difference from control significant at the 5-percent level.

and 42 percent for the unreleased trees, but by the autumn of 1956 the live-crown ratio of released trees increased to 47 percent, while that of unreleased trees decreased to 37 percent. Wiring significantly increased the live-crown ratio of released trees, but it decreased live-crown ratio of unreleased trees. Girdling increased live-crown ratio of released trees, but it did not seem to affect the live-crown ratio of unreleased trees.

At the beginning of the experiment, average lateral crown area per tree was 193 and 219 square feet for released and unreleased trees, respectively. By the end of 1956 the average lateral crown area for released trees increased to 318 square feet, while that for unreleased trees decreased to 206 square feet. Except for the significant decrease in lateral crown area of wired unreleased trees, stem treatments did not affect lateral crown area of either released or unreleased trees.

Effect of Treatments on Food Reserves

Methods

Twig samples for determination of total nitrogen and of stored carbohydrates were collected in the late winter of 1954-55. Samples consisted of 1- to 2-year-old twigs from branches growing in the third whorl from the tip on the northwest side of the crown. It was assumed that only food stored in the bark and wood tissue of the young twigs could affect cone production, since extensive studies by Curtis (1920) indicated that carbohydrates translocated to the main stem or roots were used close to the place of storage, and did not return to the shoots.

Twig samples were dried at 90° C for 72 hours. The needles were then discarded and the stems ground in a Wiley mill using a 40-mesh screen. The ground material was stored in glass containers at room temperature until the summer of 1956 when the chemical analyses were made.

Total nitrogen was determined by a modified Kjeldahl method (Emerson, 1925). Reserve carbohydrates, including starch, sugars, and their intermediate products, were hydrolyzed to glucose with the commercial enzyme preparation "Clerase." The amount of glucose in the final solution was determined by the method of Whitmeyer-Hassid which involves titration against 0.01N solution of ceric sulfate using Setopaline C indicator (Joslin, 1950). Total nitrogen and reserve carbohydrates were expressed as percentage of oven-dry weight.

Results

One- to 2-year-old twigs of released control trees contained about 5 percent less reserve carbohydrates than did corresponding twigs of control unreleased trees (Table 5). It is assumed that the relatively low carbohydrate reserves in the released trees were primarily caused by the drain of increased seed production.

There was no indication that either girdling or strangulation affected the amount of reserve carbohydrates. The values for individual trees ranged between 6.0 and 11.7 percent for both released and unreleased trees, but were grouped usually between 8 and 9 percent.

Total nitrogen in twigs of released trees averaged 22 percent higher than in twigs of unreleased trees. The highest and the lowest values were 0.60 percent and 0.30 percent for the released and 0.52 percent and 0.15 percent for unreleased trees. Stem treatment did not affect amount of total nitrogen in twigs of released or unreleased trees.

The average carbon-nitrogen ratios for released and unreleased trees were 19 and 25 respectively, ranging between 14 and 30 for released trees and between 13 and 56 for unreleased trees.

Effect of Crown Release on Available Light and Soil Moisture

Methods

Light intensity was measured with a Weston illumination meter under the crown canopy of each fifth tree on July 11, 1956, which was sunny. Four measurements,

TABLE 5. Stored carbohydrates and total nitrogen in 1- to 2-year-old twigs expressed as percentage of oven-dry weight.

Treatment	Stored carbohydrates in percent	Total nitrogen in percent	Carbon-nitrogen ratio
Girdled			
Released	8.33	0.441	19.3
Unreleased	8.59	0.376	23.6
Wired			
Released	8.13	0.460	17.9
Unreleased	8.55	0.358	26.2
Banded			
Released	8.19	0.429	19.7
Unreleased	8.46	0.370	23.5
Control			
Released	8.18	0.436	19.1
Unreleased	8.57	0.357	26.1

distributed evenly on the edge of the crown projection and 5 feet above the ground, were made hourly between 9:30 am and 3:35 pm. While light measurements were taken under the crown canopy, full light intensity was recorded hourly in an open area adjoining the experimental stand.

In the spring of 1955 one Bouyoucos moisture block was buried 6 inches deep in the soil under the southwest edge of the crown projection of each fifth tree. This design made it possible to place a moisture block under one of the five trees in each experimental block with random representation of the treatments.

Soil moisture measurements were made weekly with a Wheatstone bridge from the beginning of June to the end of September during 1955. When dry periods occurred soil moisture content was measured every few days in an effort to record the number of days when soil moisture was at or near the wilting percentage.

Results

Light. Light intensities under the crowns of released and unreleased trees are given in Table 6. Between 8:30 am and 3:30 pm on a clear day in July the light intensity under released trees averaged 58 percent of the light intensity recorded in an open field. Light intensity under unreleased trees averaged 42 percent of the intensity in an open field. The difference between average light intensity under the canopy of released and unreleased trees was

TABLE 6. Variations in light intensity under tree crowns at various times of the day on July 11, 1956. Light intensities expressed as percentage of the light intensity in an open field.[1]

Time interval	Released trees	Unreleased trees
	Percent	*Percent*
8:43– 9:52 am	60.2	37.0
10:10–11:15 am	60.9	43.8
11:34 am–12:51 pm	63.5	52.9
1:10–2:11 pm	68.1	48.0
2:38–3:26 pm	46.1	29.8
8:43 am–3:26 pm	58.0	42.3

[1]Each value represents an average of four readings under 22 trees.

23 percent points between 8:30 and 9:30 am, it decreased to 10 percent points between 12 noon and 1:00 pm and gradually increased again in the afternoon up to 16 percent points between 2:30 and 3:30 pm.

The extreme light intensities under individual crowns were 44 and 73 percent for the released trees and 27 and 61 percent for the unreleased trees.

Soil moisture. Variations in soil moisture content under the crown canopy of experimental trees over a period of 110 days during the summer of 1955 are given in Table 7. The soil in the released and unreleased portion of the stand was at or above field capacity only immediately after rain or during a prolonged rainy spell. At other times the soil moisture was consistently higher in the released than in the unreleased portion of the stand. The differences were particularly great during dry periods.

TABLE 7. Variations in soil moisture content at a 6-inch depth on different dates. Observations taken under the same crown canopy during the summer of 1955.[1]

Date (1955)	Soil moisture (percent of oven-dry weight)	
	Released trees	Unreleased trees
	Percent	*Percent*
June 13	6.6[2]	6.5
June 17	4.8	3.2
June 22	6.5	6.6
July 1	3.2	2.5
July 5	2.5	2.3
July 13	3.8	3.2
July 20	6.0	5.8
July 27	2.8	2.4
Aug. 1	6.3	6.4
Aug. 8	3.0	2.5
Aug. 22	11.0	11.0
Aug. 30	10.2	10.0
Sept. 30	10.8	10.8

[1]Each value represents an average of 22 observations.

[2]Approximate field capacity = 10 percent; approximate wilting percentage = 2.5 percent.

In general, unreleased trees were exposed to much greater fluctuation in available soil moisture than were released trees. During the 110 days of observation 6 inches of top soil under released trees remained at field capacity for 79 days, at intermediate moisture conditions for 26 days, and at or near wilting percentage for 5 days. The corresponding values for unreleased trees were 74, 26, and 9 days.

Only under 9 of 22 released trees did the soil moisture ever reach the wilting percentage, while the roots of 18 out of 22 unreleased trees remained for 4 or more days in soil at the wilting percentage. Soil moisture under several released trees remained at or near field capacity during the entire growing season. On the other hand the soil under some unreleased trees remained at or near the wilting percentage for 23 days. It should be noted that these 23 days represent the cumulative value for the entire growing season and were distributed over three dry periods in July and early August.

Tree Characteristics Correlated with Cone Production

Methods

The logarithm of the combined 1954 and 1955 cone crops of each tree was considered as dependent variable y, while the following seven tree characteristics were analyzed as independent variables:

X_1 = Logarithm of the number of cones produced in the period 1951 to 1953

X_2 = Diameter at the breast height in April, 1952 in inches

X_3 = Lateral crown area in April, 1952 in square feet

X_4 = Percentage of nitrogen in bark and wood tissue of 1- to 2-year-old shoots, collected in winter of 1954-55 from the third whorl from the tip and expressed on the basis of oven-dry weight of analyzed tissue

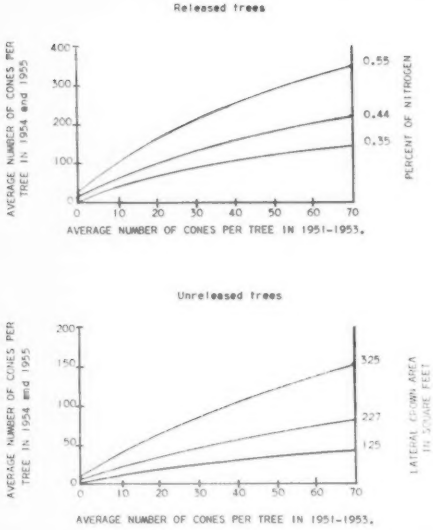

FIGURE 2. *Tree characteristics correlated with cone production in 1954-1955.*

X_5 = Percentage of carbohydrate reserves in winter of 1954-55 in the 1- to 2-year-old shoots expressed in terms of glucose on the basis of oven-dry weight of the analyzed tissue

X_6 = Ratio of X_5 to X_4 (carbon-nitrogen ratio)

X_7 = Ratio of the diameter one inch above the treatment to diameter at breast height in autumn of 1956

Results

Multiple regression analyses revealed that X_1 and X_4 were significantly correlated with cone production of released trees, while X_1 and X_3 were significantly correlated with cone production of unreleased trees. The resulting equations were as follows:

Released trees: $\text{Log } (y + 1) = 0.534 + 0.543X_1 + 1.789X_4$

Unreleased trees: $\text{Log } (y + 1) = -0.062 + 0.700X + 0.0029X_3$.

Cone production of released and unreleased trees during 1954-1955 was highly correlated with previous fruitfulness (Fig. 2.). In addition, cone production of the released trees was correlated with the amount of nitrogen in bark and wood tissue of 1- to 2-year-old shoots in the upper part of the crown, while cone production of the unreleased trees was correlated with the lateral crown area of the trees.

Discussion

A sevenfold increase in cone production of released trees during the third growing season and a fourfold increase during the fourth growing season, following crown release is attributed to the modified environment induced by the treatment. The entire crowns of the released trees were exposed to high light intensity. The roots had more growing space and consequently larger areas supplying them with mineral nutrients, nitrogen, and soil moisture. The reduced root competition also increased the amount of available soil moisture per tree, while the rapidly decomposing slash and litter probably increased the amount of nitrogen and minerals available to the released trees.

Thus the released trees were benefited by higher light intensities, more available soil moisture, by fewer and shorter periods of critical soil moisture, and probably by a higher amount of available nitrogen and mineral nutrients. Since loblolly pine requires full sunlight (Kramer and Decker, 1944) and adequate soil moisture (Kozlowski, 1949) for maximum rates of photosynthesis, the released trees were able to synthesize enough food for luxurious vegetative growth and abundant seed production. The abundance of food in the released trees during the period of experimentation was manifested by almost a doubling of the average lateral crown area, a high rate of diameter growth, and a relatively high production of cones. Supposition that insufficient reserve of nitrogen rather than of carbohydrates was the limiting factor in cone and seed production of released trees is supported by findings of

Potter and Phillips (1930), who concluded that carbohydrate levels of normally exposed plants are not critical for growth and fruiting, provided a certain amount of nitrogen is available.

Decreased light intensity and frequent shortage of available soil moisture in the unreleased portion of the stand probably resulted in a relatively low rate of photosynthesis and subsequent shortage in food. The inadequacy of food supply in unreleased trees was reflected in the decreased live-crown ratio and lateral crown area. It appears that unreleased trees were not able to synthesize enough food for both vegetative growth and prolific seed production. Consequently, any increase in the lateral crown area of the unreleased trees was accompanied by increased production of cones and seed. It is therefore assumed that food shortage was the limiting factor in cone production of the unreleased trees in 1954 and 1955.

The results of this experiment are in close agreement with the findings of Barrett (1940), Pomeroy and Korstian (1949), Trousdell (1950), Wenger (1953 and 1954), Lotti (1953), Easley (1954), and Girgidow (1956). These investigations emphasized the immediate effect of crown release on flower-bud formation manifested by abundant cone crops in the third growing season following treatment.

Girdling and strangulation interfere with normal physiological processes in the trees, and are believed to stimulate fruiting by concentrating carbohydrates in the upper parts of trees. Stimulation of fruiting is supposed to be proportional to the degree of interference with the downward flow of food in the phloem and should decrease in the order of girdling, wiring, and banding. Indeed, though statistically not always significant, cone production of released and unreleased trees followed the expected pattern, being highest for the girdled and lowest for the banded trees.

Girdling and strangulation favor seed production at the expense of vegetative growth and development. Regirdling and severe strangulation cause starvation of the roots, decrease vegetative growth, and eventually cause death of treated trees. In the present experiment the death of one banded and two wired trees probably was the result of dehydration caused by inadequate absorption by starved roots.

The inhibitory effect of wiring and girdling on growth was particularly noticeable in the unreleased portion of the stand where carbohydrates and soil moisture supply were more critical than in the released portion. By the end of 1956 wired, unreleased trees had the smallest crown area and the lowest live-crown ratio of all experimental trees. More growth suppression resulted in wired trees than in girdled probably because the wires which were tightened in 1952 remained on the trees until the winter of 1954-55, while the incisions on the girdled trees were fully overgrown by the end of 1953 growing season.

The detrimental effect of girdling and strangulation on growth and development of trees was reported by Arnborg (1946), Bergman (1955), and Girgidow (1956).

In 1954 trees banded and released produced as many cones as did untreated released trees, but in 1955 they lagged considerably behind all other trees in cone and seed production. Banding, moreover, suppressed cone and seed production of unreleased trees. Holmes and Matthews (1951) also reported that metal bands failed to stimulate flower-bud formation in Corsican pine during the first growing season following treatment, but they caused peculiar coloration of the bark. The effect of banding on cone production and other aspects of tree physiology deserve further study.

The large number of viable seeds per cone in released trees probably resulted from an abundance of pollen as well as a high degree of cross-pollination. The amount of pollen in the unreleased portion of the stand was relatively small, and the chance of cross-pollination was also small

because of the few flowering trees and interference with free movement of pollen by the dense crown canopy.

The higher number of viable seeds per cone in the upper part of the crowns is believed to be the result of the abundance of pollen in general and of the greater chance of cross-pollination in the upper crowns. Rempe (1937) demonstrated that in forest stands the amount of pollen in the air decreased very rapidly from the tree tips toward the crown bases. Dengler (1932), and Plym-Forshell (1953) reported on the superior viability and germination of Scotch pine seed originated from the cross pollination, while Acatay (1938) found that seeds collected from the tips of Scotch pine trees had higher germination percentage than seeds from other parts of crowns.

Possibly some loblolly pine trees have inherited capacity for high seed production while others do not have this capacity. Regardless of treatment, in the present experiment, cone production of pine trees in 1954-55 was highly correlated with cone production during the three previous years. Several trees produced over 300 cones each although their morphological development was only average or even less. One released tree with a well developed crown and higher than average diameter did not produce a single cone during 6 years of observation. Pomeroy and Korstian (1949) and Grano (1958) also concluded that some loblolly pine trees had an inherent capacity for abundant seed production.

Generally, only well developed crowns and root systems insure abundant and continuous production of viable seed. The best long-term increase in seed production is achieved by heavy thinnings, which allow the crowns to develop more fully than in closed stands.

Application of Results in Silvicultural Practice

Cone and seed production of pulpwood-size loblolly pine trees can be increased considerably by full crown release a few years prior to final harvest cutting. A 25-year-old loblolly pine tree 9 to 10 inches d.b.h. may produce up to 3,400 viable seeds in some years if its entire crown had previously been exposed to full sunlight for at least three growing seasons. In young loblolly pine stands the earlier that full crown release occurs, the higher the seed production.

Girdling and strangulation are less effective in stimulating seed production in pulpwood-size loblolly pine trees than is full crown release. When used as a supplement to crown release, girdling and strangulation are likely to be more harmful than helpful. Their beneficial effect on seed production is negligible, and the risk of losing trees to storm breakage or root starvation is high.

Full crown release may be considered a biologically sound and economically profitable silvicultural practice because it not only increases seed production but also accelerates growth. This practice makes it possible to grow loblolly pine on a pulpwood rotation and still benefit from the advantages of natural regeneration without additional cost.

Preharvest crown release can readily be combined with thinning at least three years prior to the final harvest for pulpwood. Even when a thinning has not been made before the harvest cutting, about 15 trees per acre could be released several years prior to harvest. The increased growth of released and of adjoining trees may in a few years offset the volume removed. Under normal conditions the removed trees would be merchantable and would provide an early income, while the better developed crowns and root systems of the released trees would insure better and more prompt seed production as well as a minimum risk of losing the seed trees from natural causes.

In selecting young trees of loblolly pine for preharvest crown release, their previous fruitfulness, crown size and crown density are the best indicators of their future seed productivity.

The present work indicates that fifteen

25-year-old seed trees per acre, when given ample growing space 4 years before harvest would be capable of producing 100,000 viable seeds in two years, an amount usually considered adequate to assure a satisfactory restocking of loblolly pine on average sites (Barrett 1940, Pomeroy and Korstian 1949, Trousdell 1950).

Summary

Beginning in 1952 a 5-year study was initiated on effects of crown release, partial girdling, wiring, and banding of stems on cone production of pulpwood-size loblolly pine trees.

Full crown release was the most successful method of stimulating cone and seed production. It resulted in a sevenfold increase in cone production the third year after release and in a fourfold increase the fourth year. Crown release almost doubled the number of viable seeds per cone and increased diameter growth and crown development.

Available light and soil moisture conditions were improved to a great extent in the released portion of the stand. The soil in the unreleased portion of the stand remained at the wilting percentage approximately twice as long as did the soil in the released portion of the stand.

Partial girdling and wiring of stems did not contribute significantly to cone and seed production of released or unreleased trees, but such treatments decreased diameter growth and reduced the live-crown ratio of unreleased trees. Banding suppressed cone production of released and unreleased trees and reduced by one-half the number of viable seeds per cone in the released trees.

In released trees cones borne on branches in the third whorl from the tip and above had more viable seeds per cone than did cones borne on the branches below the fourth whorl from the tip.

Regardless of treatment, cone production of experimental trees in 1954-55 was positively correlated with cone production in 1951-53. In addition to previous fruitfulness, cone production of released trees in 1954 and 1955 was also positively correlated with the amount of nitrogen in the bark and wood of the 1- to 2-year-old twigs in the upper part of the crown. The lateral crown area was positively correlated with cone production by unreleased trees in 1954 and 1955.

Neither the total amount of carbohydrate reserves in the bark and wood of 1- to 2-year-old twigs in the upper part of the crowns, nor the carbon-nitrogen ratio during the winter of 1954-55 was significantly correlated with cone production in 1954 and 1955.

Application of results in silvicultural practice was discussed, and preharvest crown release was recommended as a biologically sound and economically profitable silvicultural practice for stimulation of seed production in pole-size loblolly pine.

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Late Flowering in Aspen and Its Relation To Naturally Occurring Hybrids

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INTEREST in naturally occurring hybrids of forest trees originates from several sources. In tree improvement programs these hybrids are of interest because, as products of hybridization (in many cases followed by back-crossing) which have survived under natural conditions, they yield some insight regarding morphology, growth rate, disease and insect resistance, climatic tolerance and wood quality which might be expected of artificially produced species hybrids of similiar parentage.

Naturally occurring interspecific hybrids have been reported by a number of workers in forestry and forest genetics. Johnson (1939) and Smith and Nichols (1941) published comprehensive reviews of interspecific hybrids of forest species and included in their lists 25 genera which contained naturally occurring hybrids. Richens (1945) and Little (1953) also have listed numerous hybrids, some of which were not included in earlier reports. More recently a number of descriptions and reports of naturally occurring hybrids have been made in the genus *Populus*. Included in these reports are descriptions and discoveries in published papers by Heimburger (1953), McComb and Hanson (1954), Pauley (1956), Little, *et al.* (1957), and unpublished information from McComb[1] Joranson,[2] and Langenbach.[3]

Flowering Characteristics of Aspen

Quaking aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.) are characteristically dioecious and stands are generally composed of intermingled clones of staminate and pistillate trees. The flowers of aspen develop from large buds located just below branch and twig terminal buds. Flower buds are normally concentrated in the upper part of the crown and on fully exposed branches in lower positions.

The flowers of aspen, like other members of the genus *Populus*, are borne in aments or catkins. Normally, elongation, anthesis and pollination of the female catkins of quaking aspen occur in northern Wisconsin during the last week in April. Following pollination, they develop rapidly, dehiscence of the capsule and release of the seed with attached cottony seed-stalk hairs beginning in approximately four weeks.

Flowering of bigtooth aspen follows a

[1]McComb, A. L. Information on recently located *Populus* hybrids in Iowa. (Private communication.) Iowa State College, Ames, Iowa. 1957.

[2]Joranson, Philip N. Naturally occurring aspen hybrid located near Ogden, Iowa. (Unpublished research.) The Institute of Paper Chemistry, Appleton, Wisconsin. 1957.

[3]Langenbach, Carl. Information on a newly discovered hybrid aspen near Farmington, Iowa. (Private communication.) Crandon Paper Mills, Inc., Fort Madison, Iowa. 1957.

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similar pattern, with elongation and pollination occurring about 10 to 12 days later than in quaking aspen.

Natural Hybrids in the Section Leuce

Artificial hybrids in the genus *Populus* outnumber those of any other tree genus, and natural hybrids have often been found. Johnson (1939) lists 121 *Populus* species hybrids, 16 of these reported in nature.

Since hybrids between bigtooth and quaking aspen can be produced with ease in the greenhouse, it appears that time of flowering and geographic isolation are the most important factors which restrain natural hybridization between these two native aspen species. The aspen-like white or silver poplar (*P. alba* L.) of Europe, and bigtooth aspen have similar flowering periods, and hybridization takes place quite commonly (Heimburger, 1953; McComb and Hanson, 1954; Little, *et al.*, 1957; McComb[4] and Langenbach[5]) when these species are grown near each other. Quaking aspen and bigtooth aspen are often found growing side by side in nature, but hybridization does not commonly take place, evidently because quaking aspen flowers 10 to 12 days earlier than bigtooth aspen, its stagmas remaining receptive for only a few days.

Several explanations have been advanced to account for the origin of a number of apparent natural hybrids between these two native species. Pauley (1956) suggested that quaking aspen growing in localities in which spring temperature inversion was common might flower late enough to permit natural hybridization with nearby bigtooth aspen growing on higher ground, and found hybrids in a location where temperature relations of this sort evidently existed. Another possible explanation, however, is the occurrence in native or inherently late-flowering quaking aspen clones of either sex. An original report of such behavior follows.

Late Flowering in Aspen

During 1956, 1957, 1958, and 1959, late-flowering catkins were observed on a number of branch collections being forced in the greenhouse during February and March. Usually, eight to ten days after producing a number of catkins at the normal flowering time, other flower buds elongated and produced a second crop of catkins on the same branches. No consistent relationship was observed regarding the relative location of late and early flowering catkins as to their position on the branches or in the tree crown. "Late flowering" as here described was observed on five female clones and one male clone of quaking aspen and on one female clone of bigtooth aspen. In some clones this behavior might properly be called "two-phase" flowering but in other instances a distinct separation between successive crops of flowers is lacking.

In two of the observed cases of late flowering the catkins were partly flower-bearing and partly vegetative. Figure 1 pictures a staminate late-flowering catkin from one of the clones and Figure 2 illustrates a typical late-flowering pistillate catkin from another clone. The proximal portions of the catkins of these two clones were flower-bearing while the distal portion was made up of numerous, crowed bractlike or leaflike appendages. The individual

[4]See footnote 1.
[5]See footnote 3.

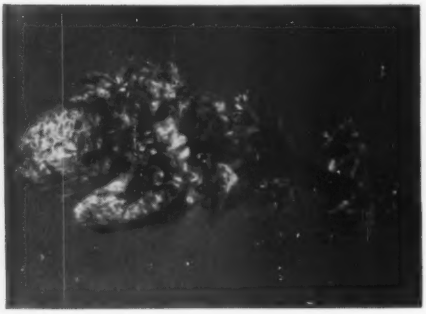

FIGURE 1. *A late-flowering staminate catkin of quaking aspen with vegetative development in the distal portion.*

flowers of the pistillate catkins (Fig. 2) were not short-stalked, as is commonly the case, but were attached to the rachis by rather long pedicels. Each individual flower was also subtended by good-sized bracts, giving it a more flowerlike appearance.

Particularly significant were quaking aspen clones which produced large numbers of late-flowering catkins on repeated branch collections made during the same year and on collections made in successive years. Flower-bearing material from one female quaking aspen (Fig. 3) for instance, produced about 60 percent normal-flowering catkins which were pollinated artificially, resulting in good seed set. Five to six days after pollination and as the first set of catkins was showing evidence of seed development, additional catkins began to elongate. Beginning 10 days after pollination of the first-appearing catkins, a total of 100 receptive late-flowering catkins was removed from this branch collection.

Another interesting example of late flowering was a collection from an outstanding female quaking aspen phenotype growing in mixtures with bigtooth aspen. Flower and flower bud collections from this tree proved to be typically late flowering both in greenhouse-forced collections and on the tree in nature. A collection of open pollinated seed made later in the spring, resulted in the production of several seedlings which had characteristics intermediate between those of bigtooth and quaking aspen. One seedling in particular was very rapid growing and had typical "quaking x bigtooth" hybrid leaf characteristics. Further morphological investigation of this parent tree and the surrounding stand is planned.

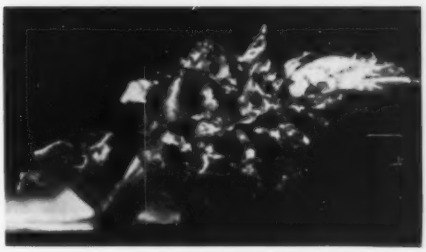

FIGURE 2. *A late-flowering pistillate catkin of quaking aspen with long-pediceled individual flowers. Note the petal-like bracts of individual flowers and the distal vegetative portion.*

FIGURE 3. *First-appearing (left) and late-flowering (right) female catkins of quaking aspen. The late-flowering catkins are in anthesis; the catkin at the left flowered 10 days earlier.*

Late flowering of quaking aspen has been observed under greenhouse conditions and verified in nature. It has also been determined that seeds are produced in abundance by the late-developing pistillate catkins, and that germination and early seedling development in the greenhouse show no impairment.

The evidence at hand therefore strongly suggests that the occurrence of late-flowering catkins as here described provides an alternative method by which the usual differences in the time of flowering between quaking and bigtooth aspen may be bridged in nature.

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Control of the Plant Environment

Edited by J. P. Hudson. Butterworth's Scientific Publications, London. Available in the United States from Academic Press Inc. 111 Fifth Ave., New York 3. 240 pp. $7.50.

Review by Stephen H. Spurr
The University of Michigan

Dealing with present-day techniques of growing plants in artificial environments, this volume contains the proceedings of a meeting on the subject (The Fourth Easter School in Agricultural Science) held at the University of Nottingham School of Agriculture in April 1957. The widespread interest in growth chambers of various sizes and the rapid technological advances in their design and operation make a meeting of this type timely and the widespread dissemination of the papers presented valuable.

The present volume emphasizes British and Dutch developments in controlling plant environments for experimental purposes. Of the more than 40 papers presented, many are published as abstracts, so that the bulk of the present book is devoted to a few papers printed in their entirety. S. J. Wellensiek from Wageningen summarizes the general state of our knowledge of the effect of environmental factors of temperature, light, and water on plant development and growth; W. W. Schwabe of Imperial College, London, is concerned with morphogenetic responses of plants in controlled environments; E. C. Wassink of Wageningen with growth responses; and P. T. Thomas of the University College of Wales, Aberystwyth, with plant genetics in controlled environments. Three other papers in part I, dealing with general effects of the environment on plants, are concerned with artificial light, wind, and agronomic aspects of environmental control.

Much of the book, however, is devoted to installations for the control of plant environments. Existing growth cabinets, growth rooms, and phytotrons are described and evaluated. Longer papers published in full deal with problems of controlling the water regime, with the capabilities of greenhouses as an environment for plants, and with the design of growth rooms.

"Control of the plant environment" will be an important source of reference for any scientist concerned with the study of environmental plant factors under controlled conditions.

Decay Associated with Woodwasps In Balsam Fir Weakened by Insect Attack

BY
M. A. STILLWELL

DETERIORATION studies being conducted on balsam fir, *Abies balsamea* (L.) Mill., killed by the spruce budworm, *Choristoneura fumiferana* (Clem.), in the Kedgwick Watershed of New Brunswick, show that fungi have penetrated the sapwood to an average depth of 0.4 inch in trees that had been dead less than a year. This is a very rapid rate of deterioration compared with that of previously examined wind-thrown trees in northern New Brunswick, in which scarcely any decay was present in the first two years after death. Although budworm-killed trees may not dry out as quickly as wind-thrown trees, resulting in more favorable conditions for decay, it was felt that this would account for only a part of the difference. Consequently, living trees in the study area were examined for possible explanation of this rapid deterioration.

Thirty living trees were selected for study in October, 1958. They had all been severely defoliated for several years by the budworm and were low in vigor. The degree of defoliation was not the same for all trees, some being in much better condition than others as to length of dead top and crown density. The trees were felled, cut into 4-foot bolts, and measurements of diameter inside bark and depth of deterioration at four points around the perimeter of log ends were made at each cut. The age at stump, diameter at breast height outside bark, and length of dead top were also recorded. Samples of deteriorated sapwood were cultured to determine the causal organisms.

Gross merchantable volume (portion between a 1-foot stump and a 3-inch top), and volume of sap rot were determined by Smalian's formula. Computations were carried to two decimal places and the resulting values were taken to the nearest tenth of a cubic foot. Volumes less than 0.05 cubic feet were called trace. The average depth of radial deterioration of the sapwood in each tree was obtained by totalling the radial depth of deterioration at each cut and dividing by the number of cuts. Values less than 0.05 inch were called trace.

Results

Stained sapwood was found in each of the 30 trees and, with one exception, was more prevalent in the lower stems. The first four-foot bolt of each tree, and the 17 to 21-foot bolt from the exceptional tree, were collected for detailed examination at the Laboratory. Cultural identifications of isolates from the stained wood of these bolts and from discs cut at other levels in the trees showed that at least many of these stains were the incipient stages of decay. Of the 274 cultures made, 80 were identified as *Stereum chailletii* Pers., 9 as *S. sanguinolentum* Alb. & Schw. ex Fr., 3 as *Corticium galactinum* (Fr.) Burt, and 4

Contribution No. 602 from Forest Biology Division, Research Branch, Canada Agriculture, Ottawa. The author is located at the Forest Biology Laboratory, College Hill, Fredericton, N. B. Manuscript received Dec. 16, 1959.

as *Armillaria mellea* (Vahl ex Fr.) Quél.[1] The remainder were either Imperfects, contaminants, or blanks (no growth).

Seven trees were partially girdled at the base by *A. mellea*. Cultural identifications or the presence of rhizomorphs between the bark and wood were the means by which this type of injury to the cambium was recognized. Decay had apparently ascended from infected roots (Fig. 1).[2]

The bolts were examined in the Laboratory to determine how the fungi entered through the apparently sound bark. Occasionally, small hardened droplets of pitch were found on the bark surface. Beneath these were found minute holes approximately 0.2 mm in diameter; these were typical of siricid borings for oviposition. However, many more borings were evident that did not exude pitch on the bark surface. The bark surrounding the borings was usually dark in color, and the discoloration increased in size and changed in shape from round to fusiform (longitudinal axis of the tree) when more bark was shaved away (Figs. 2 and 3). The borings penetrated the outer sapwood; streaks of decay were associated with them and the focus of infection by the causal fungi appeared to be in their vicinity (Figs. 4 and 5).

Numerous pieces of wood (approximately 1 inch square) containing the insect punctures were cut from the bolts. The wood was shaved off the radial plane to expose the depth and direction of the puncture and its contents. The depth of the punctures in the wood varied from 2 to 5 mm and the direction was approximately at right angles to the surface. A few borings were empty, but many contained one or sometimes two eggs; the remainder contained small siricid larvae approximately 1 mm in length. Larger larvae in later stages of development were also found in galleries usually situated at right angles to the oviposition holes (Fig. 6). In one bolt (Tree No. 15, Table 1) a few pupae were located just under the surface of the wood. The bolt was enclosed in a polyethylene bag to prevent drying out and set aside for emergence of adults. In seven weeks six male woodwasps emerged (January 30), followed in three weeks by one other male woodwasp of a different species. The first six were identified as *Xeris spectrum* (L.) (Fig. 7), the other as *Sirex cyaneus* F. (Hymenoptera: Siricidae).[3] In Ontario three siricids, *S. cyaneus*, *Sirex* sp. (*noctilio* group), and *Urocerus albicornis* F. have been found in trees newly dead from budworm defoliation (Belyea 1952).

Several bolts contained a few Coleopterous larvae but stain was rarely evident in the vicinity of the galleries.

The average radial penetration of sapwood decay for the 30 trees was only 0.04 inch. However, the depth of many individual streaks extended at least one inch into the sapwood, although most were approximately 0.5 inch deep (Fig. 8). The volume occupied by this firm sapwood decay amounted to 2 percent of the total gross merchantable volume (Table 1).

To determine if the above situation existed elsewhere a survey was conducted of balsam fir severely defoliated by budworm in other localities throughout northern New Brunswick. Trees weakened by the balsam woolly aphid (*Adelges piceae* Ratz.) in other parts of New Brunswick were also examined for siricid oviposition punctures.

Siricid punctures were found in weakened trees at all localities visited (Fig. 9). Isolates from stained sapwood and discolored bark surrounding the punctures were obtained from at least one tree in each

[1]Identifications by Mrs. E. K. Hoyt, formerly Assistant Technician, Forest Biology Laboratory, Fredericton, N. B. Six *S. chailletii* cultures and three of *C. galactinum* were confirmed by M. K. Nobles, Plant Research Institute, Research Branch, Canada Agriculture, Ottawa.

[2]All photographs by B. E. Bates, Forest Biology Laboratory, Fredericton, N. B.

[3]Identifications by G. S. Walley and O. Peck, Entomology Research Institute, Research Branch, Canada Agriculture, Ottawa.

locality except Nictau, where one tree weakened by successive budworm defoliation was felled and the entire stem brought into the Laboratory for examination. Siricid oviposition punctures were found from the ground level almost to the top of the tree. Isolates were only obtained from stained sapwood in the vicinity of 209 punctures and 179 of the resulting cultures were identified as *Stereum chailletii*; the remainder did not grow. From the other localities *S. chailletii* was isolated 46 times from sapwood and 20 times from bark. Ten miscellaneous fungi were also isolated, three from sapwood and seven from bark (Table 2).

TABLE 1. Amount of decay in trees weakened by spruce budworm defoliation in northern New Brunswick.

Tree No.	D.B.H.	Age at 1-foot stump	Length of dead top	Gross merchantable volume	Volume firm sap decay	Av. firm radial penetration
			Feet	*Cu. ft.*	*Cu. ft.*	*Inches*
1	5.1	78	10	2.3	0.1	0.1
2	4.7	76	2	1.3	0.1	0.1
3	7.7	85	2	7.5	0.1	trace[4]
4	8.8	83	2	10.7	trace[3]	trace
5	9.6	84	10	13.3	0.4	0.1
6	6.6	67+[1]	1	4.2	0.2	trace
7	7.3	66+	2	4.2	trace	trace
8	5.3	72	2	1.6	0.1	0.1
9	5.9	80	3	2.7	trace	trace
10	5.0	78	10	1.8	0.1	trace
11	5.6	72	10	2.3	trace	trace
12	4.9	53+	12	1.6	0.1	0.1
13	8.3	82	10	8.6	0.4	0.1
14	6.7	73	2	4.6	0.1	trace
15	7.1	85	8	5.6	0.2	0.1
16	6.7	68+	12	3.4	trace	trace
17	4.9	88	10	1.1	trace	0.1
18	6.1	71	1	2.9	0.2	0.1
19	6.2	90	6	3.3	0.1	trace
20	6.0	92	1	2.7	0.1	0.1
21	7.7	88	3	6.4	0.2	trace
22	7.7	74+	5	6.5	0.4	0.1
23	5.7	...[2]	4	2.0	trace	trace
24	8.1	77+	8	6.5	trace	trace
25	7.6	88	3	6.4	trace	trace
26	7.4	81	2	5.6	0.1	trace
27	7.5	93	1	5.7	trace	trace
28	8.6	84	3	8.2	trace	trace
29	10.6	90	14	12.7	0.4	0.2
30	5.6	84	10	4.0	trace	trace

[1]Total age undetermined because of heart rot.
[2]Age unknown.
[3]Less than 0.05 cubic foot.
[4]Less than 0.05 inch.

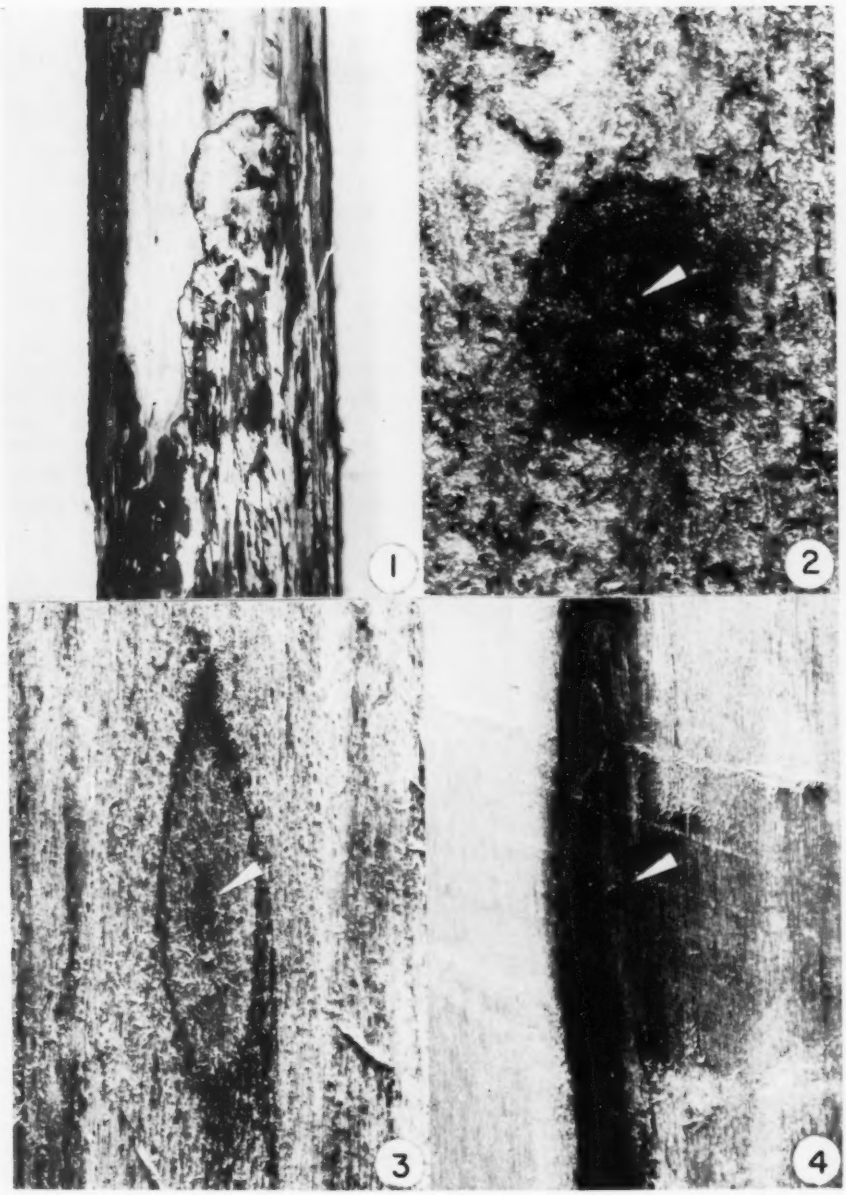

FIGURE 1. *Portion of base of balsam fir trunk partially girdled by* Armillaria mellea. *The bark has been removed to show the white mycelial fan produced by the fungus.* × *1/7.* FIGURE 2. *Discoloration in outer bark of balsam fir around insect puncture (indicated by arrow).* × *12.* FIGURE 3. *Discoloration in inner bark of balsam fir around insect puncture (indicated by arrow).* × *8.* FIGURE 4. *Streak of decay in outer sapwood of balsam fir apparently originating at insect puncture (indicated by arrow).* × *8.*

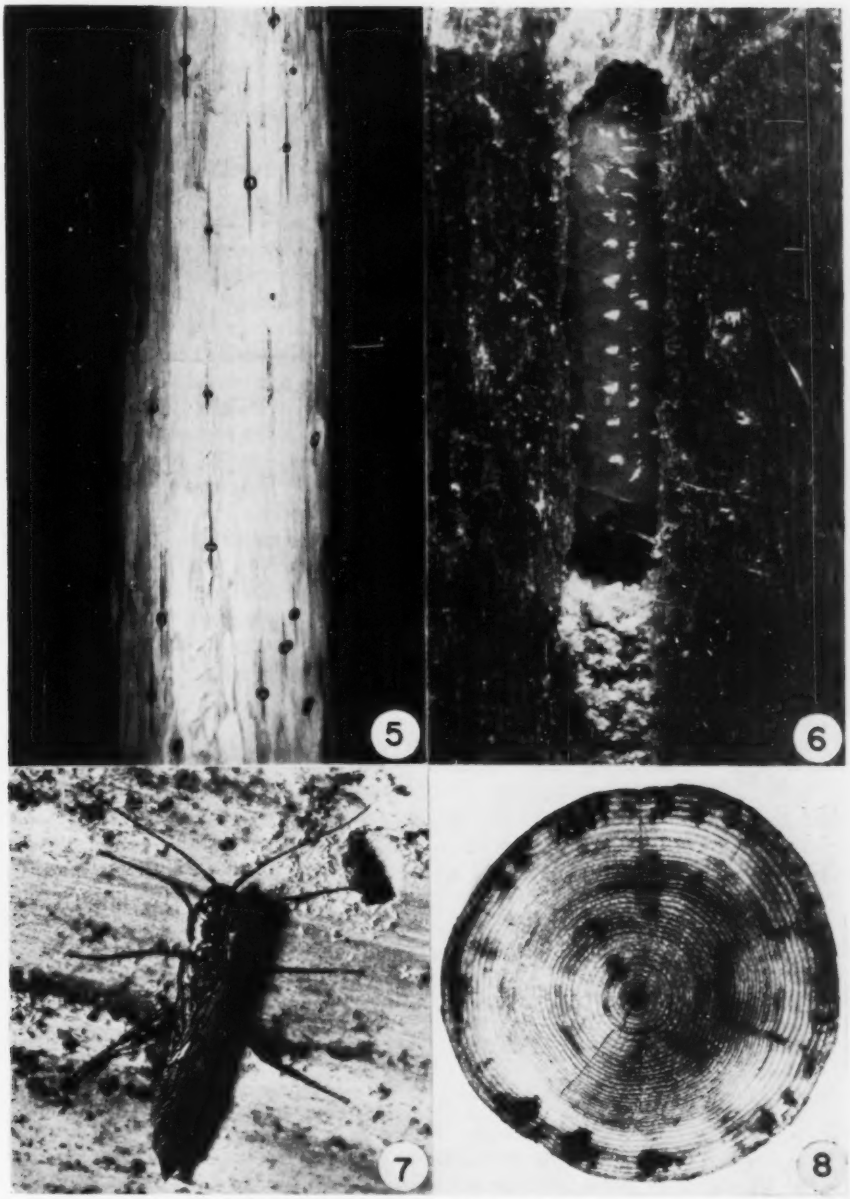

FIGURE 5. *Portion of balsam fir trunk showing streaks of decay in outer sapwood apparently originating from insect punctures. The punctures are circled.* × 1/7. FIGURE 6. *Siricid larva in decayed balsam fir wood. Note characteristic anal spine and tightly packed frass.* × 12. FIGURE 7. *Adult woodwasp, male* Xeris spectrum, *that emerged from decayed balsam fir wood. The emergence hole is at the right of the insect.* × 3. FIGURE 8. *Cross section of balsam fir trunk showing patches of decay that apparently originated at insect punctures.* × 1/5.

FIGURE 9. *Location of trees examined for siricid oviposition punctures: 0 — Detailed study area; 1-5—Budworm-weakened trees; 6-14—Trees weakened by woolly aphid.*

One could, therefore, conclude that *S. chailletii* is by far the most common wood-destroying fungus associated with siricid oviposition borings.

Discussion

Stereum chailletii and *S. sanguinolentum* are well known wood-destroying fungi of considerable economic importance in the Atlantic provinces of Canada. Deterioration studies on budworm-killed balsam fir continue to reveal the importance of these fungi; however, they become established more rapidly in this type of tree than in trees killed by other agencies. The above analysis of trees weakened by budworm defoliation and balsam woolly aphid attack showed *S. chailletii* to be particularly well established in the bark and sapwood before death, apparently having been introduced by siricids.

The relationship between the insects and fungi has not been determined, but it may be one of symbiosis. According to Parkin (1942), symbiosis between siricids and fungi was first described by Buchner in 1928 and investigated later by others. These workers have traced the history of the associated fungus almost completely through the egg, pupal, and adult stages of the insect. Parkin found modifications of the larval integument, which he termed hypopleural organs, on the posterior aspect of the first abdominal segment. These contained a fungus which was identified as

TABLE 2. Cultural results of isolates obtained from stained sapwod and discolored bark surrounding oviposition borings in balsam fir trees weakened by spruce budworm and balsam woolly aphid attack.

No.[1]	Locality	Isolates from		*S. chailletii*		Miscellaneous fungi	
		Bark	Sapwood	Bark	Sapwood	Bark	Sapwood
1	Bathurst	6	1	0	4	0	1
2	Campbellton	5	0	1	6	0	0
3	Ludlow	7	6	1	2	0	0
4	Nictau	0	30	0	179	0	0
5	Renous	5	3	2	5	1	0
6	Coal Branch Station	3	0	1	4	0	0
7	Fredericton	1	1	1	2	1	0
8	Grande-Anse	2	0	7	9	0	0
9	Grand Lake	3	2	0	2	1	0
10	Loggieville	4	0	5	9	0	0
11	Skiff Lake	5	6	0	0	1	0
12	St. John	5	4	0	0	1	2
13	St. Stephen	2	4	2	2	2	0
14	Teahan's Corner	4	3	0	1	0	0

[1]Nos. 1 to 5 budworm-weakened trees; Nos. 6 to 14, trees weakened by woolly aphid.

Stereum sanguinolentum. Further investigations, in collaboration with I. W. Varty, Forest Zoology Investigations, Forest Biology Laboratory, Fredericton, N. B., are being carried out here to determine whether symbiosis exists between one or more species of these insects and wood-destroying fungi.

For many years *Sirex* spp. have been found in dying trees in New Zealand and were regarded as secondary. In 1948 Rawlings suggested that *Sirex noctilio* F. and its associated fungus (*Stereum* sp.) were actually the direct cause of death of *Pinus radiata* D. Don in New Zealand (Rawlings, 1948). However, continued investigations led him to the conclusion that certain predisposing factors must first occur. Rawlings (1957) states that "the epidemic outbreak of *Sirex noctilio*, which culminated in 1949, was almost certainly made possible by the 1946 drought, which had the effect of reducing the water content of stems to a point favourable for the symbiotic fungus carried by the insect."

From the present study it is not difficult to realize the importance of siricids. Their apparent ability to transmit wood-destroying fungi to weakened trees presents a real problem to salvage operators. Not only must deterioration since death be considered, but also the advance of decay before death must now be weighed. Furthermore, the importance of siricids in causing death of weakened trees must be assessed. Alone they may do little damage but in association with fungi may cause death, as *Sirex noctilio* and associated fungi do in New Zealand.

Summary

Studies on balsam fir killed by the spruce budworm showed that wood-destroying fungi had penetrated the sapwood to an average depth of 0.4 inch within a year of death. Similar deterioration studies on windthrown balsam showed that decay was negligible two years after they were blown down. In an effort to explain this difference, 30 trees, weakened by budworm defoliation, were examined. *Stereum chailletii* and *S. sanguinolentum* were found in the sapwood of these living trees, apparently having been introduced by siricids. *Stereum chailletii* was also isolated from the discolored bark and stained sapwood surrounding siricid oviposition punctures in trees severely weakened by balsam woolly aphid attack. The importance of siricids as vectors of wood-destroying fungi is discussed.

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Reprints of List of Forestry Theses Compiled by Oregon State College

Reprints of the list of forestry theses published on pages 292 to 304 of this issue of FOREST SCIENCE are not now available. However, the type has been held by the printer and anyone wishing to order reprints at $1.00 per copy should write the Society of American Foresters, Mills Building, Washington 6, D. C., advising of needs. If the demand is sufficient, reprints will be printed. If not, then those needing copies of the theses list may obtain them by purchasing individual copies of the September issue of FOREST SCIENCE at $2.00 per copy.

Gibberellic Acid-Induced Growth Of Dormant Hardwood Cuttings

BY
PHILIP R. LARSON

GIBBERELLIC ACID has been shown to induce a diversity of growth responses. In trees and other woody plants the most phenomenal response has been the increased vegetative growth of young seedlings (Marth *et al.*, 1956). Another effect of potential interest and value to forest research is the ability of gibberellic acid to promote the break of bud dormancy in certain species of woody plants.

Previous studies regarding the effect of gibberellic acid in breaking the rest period of woody plants have been conducted on buds exhibiting a wide variety of dormancy conditions. Donoho and Walker (1957) demonstrated that 2-year-old peach trees, which had received only part of the normal chilling requirement, could be induced to break dormancy by sprays of gibberellic acid in water. Peach buds on winter twigs were also shown to respond when placed in a gibberellic acid solution (Velsicol Chemical Corp., 1957). Similarly, gibberellic acid-treated terminal buds of oak and maple, which had received sufficient cold exposure but had not yet broken dormancy, were stimulated to elongate 1 to 2 weeks earlier than untreated ones (Marth *et al.*, 1956).

Barton (1956) described a dormancy condition in which physiologic dwarfs of *Malus arnoldiana* seedlings were produced by embryos which had not received pretreatment at low temperatures. Applications of gibberellic acid promoted internode extension and eliminated the dwarfed condition.

Dormancy, induced and maintained by short-day conditions, was effectively broken in camellia plants by periodic applications of gibberellic acid; Coulter pine and bigcone spruce failed to respond (Lockhart and Bonner, 1957). These same authors cited a study by Lona (1957) in which cuttings of European beech, maintained in a dormant condition by short-day treatment, resumed growth following gibberellic acid applications.

Under certain conditions of dormancy and methods of application there is no response to gibberellic acid treatment. Bradley and Crane (1957), for example, reported that the dormancy of the buds on spur shoots of apricot was not broken by gibberellic acid sprays. Treatment in this case occurred when the terminal buds of the long shoots were still active, whereas those of the spurs had already entered their rest phase. Differential response to methods of application was observed by Shafer and Monson (1958), who successfully activated quiescent crown buds in leafy spurge by aqueous sprays of gibberellic acid, but not by applications in lanolin paste.

This report describes a study in which gibberellic acid promoted bud growth on dormant hardwood cuttings after exposure

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to a normal winter environment, but prior to bud burst in the spring. The term dormancy will be used here in its broadest sense, as in Doorenbos' (1953) definition: "any case in which a tissue predisposed to elongate does not do so."

Materials and Methods

Dormant cuttings of red maple (*Acer rubrum* L.), quaking aspen (*Populus tremuloides* Michx.), and Bebb willow (*Salix bebbiana* Sarg.) were collected in early April of 1957 and immediately trimmed so that all of the cuttings within each species retained the same number of lateral buds. All cuttings were taken from the central portion of the shoots where internodes of uniform lengths could be obtained. However, since the trimmed cuttings unavoidably varied to some degree in both length and diameter, they were separated into size classes and the cuttings within each size class randomized among treatments—10 cuttings per treatment.

The growth regulators, gibberellic acid (GA), 2, 3, 5-triiodobenzoic acid (TIBA), and 3-indole-acetic acid (IAA), were each dissolved in a small quantity of ethyl alcohol and made up to concentrations of ¼ percent, ½ percent, and 1 percent in lanolin by weight. The lanolin mixtures were applied to the apical cut surfaces of the cuttings, in a quantity varying with the size of the cutting. All of the applications were generous since lanolin tends to contract, leaving the cambial surfaces exposed and dry. For each species there were 2 controls, lanolin alone and no lanolin, in addition to the 9 treatments consisting of 3 concentrations of each of the 3 growth regulators. The cuttings were kept in tap water, changed semiweekly, in a greenhouse maintained at approximately 62° F night and 72° F day temperature.

Data were collected three times per week beginning with the first indications of bud burst. The observations consisted of the number of buds in each of three developmental stages for each bud position on the cuttings. The developmental stages were arbitrarily defined as follows:

Stage *a*—Green leaf tips barely visible at bud apex.

Stage *b*—Green leaves of bud fully exposed, but still furled.

Stage *c*—First leaves unfolding.

A second experiment was designed to test the effect of GA on buds exposed to only a partial winter environment. Cuttings were collected on January 9, 1958. These cuttings were handled in the same manner as the April 1957 test, but with only two treatments—1 percent GA in lanolin and lanolin control. Cuttings were collected from juvenile stump sprouts and root suckers and also from mature trees of red maple, quaking aspen, paper birch (*Betula papyrifera* Marsh.), bigtooth aspen (*Populus grandidentata* Michx.), and northern red oak (*Quercus rubra* L.) and from mature trees only of boxelder (*Acer negundo* L.), butternut (*Juglans cinerea* L.), and pin cherry (*Prunus pensylvanica* L.f.).

Spring Collection Results

Red maple. Cuttings were collected from 1- and 2-year-old stump sprouts on April 3, 1957. Three lateral bud pairs were retained on each cutting. Internodes averaged 3 to 5 inches in length.

The first break of dormancy of the uppermost lateral bud pair (hereafter referred to as the apical bud pair) was recorded on the GA-treated cuttings on April 9. By April 11, 100 percent of the GA-treated cuttings had broken dormancy. On this date, the number of apical bud pairs that had broken dormancy in each treatment is shown in Table 1.

One-hundred-percent bud burst was not attained in the TIBA-treated and the two control groups until April 17; it was delayed until April 23 in the IAA-treated group.

The final observations were made on April 30. Data for three observation dates, on the basis of stage *c* development only, are shown in Table 2. These data indicate that GA brought about a more rapid break of dormancy and consequently more rapid

TABLE 1. Number of active apical buds at time of 100-percent bud break in GA-treated cuttings.

Treatment[1]	Number of active apical buds		
	Red maple	Quaking aspen	Bebb willow
GA	30	30	29[2]
TIBA	14	7	3
IAA	--	3	--
Lanolin	1	1	1
No lanolin	1	--	--

[1]All concentrations within a treatment combined; 30 buds per treatment.
[2]One apical bud injured accidentally.

leaf expansion of the apical bud pairs than did normal greenhouse conditions alone. On the other hand, GA tended to inhibit the development of the second pair of lateral buds. This inhibition was not only evident in the delayed break of dormancy, but also in the slower development and size of the expanding leaflets. The inhibition appeared to increase with increasing concentrations of GA.

The apical bud pair of the TIBA-treated cuttings developed normally with respect to the controls, but the second bud pair developed more rapidly. In these lateral buds on the treated cuttings, the break of dormancy closely coincided with that of the apical buds and the delay in development was not overly great. By April 30, only 2 of the 30 No. 2 bud pairs had failed to reach stage *c*.

The break of dormancy and the development of both bud pairs No. 1 and No. 2 were delayed in the IAA-treated cuttings. By April 19, bud development was considerably behind that of the controls although little difference remained by April 30.

With the exception of a slight trend in the development of the No. 2 buds in the GA-treated cuttings, there appeared to be no concentration differences within treatments.

Quaking aspen. Cuttings were collected from 1- and 2-year-old root suckers on April 5, 1957. Six lateral buds were retained on each cutting. Internodes averaged 1½ to 2½ inches in length.

The break of dormancy of the apical buds was similar to that of red maple, but the differences among treatments were not as pronounced. All buds were still dormant on April 12, although 18 GA-treated buds were recorded as approaching stage *a*. The number of apical buds in each treatment that had broken dormancy by April 15 is shown in Table 1. One-hundred-percent bud burst (stage *a*) was attained in the GA-treated cuttings by April 15; all other treatments attained 100 percent on April 19.

TABLE 2. Number of red maple bud pairs attaining stage c.

Date and bud No.[1]	Treatment										
	GA			TIBA			IAA			Lanolin	No lanolin
	¼%	½%	1%	¼%	½%	1%	¼%	½%	1%		
April 12											
No. 1	5	4	4	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	--	--	--	--	--
April 19											
No. 1	10	10	10	10	6	5	5	2	3	9	7
2	2	--	--	6	4	6	2	2	2	1	5
April 30											
No. 1	10	10	10	10	10	10	10	9	8	10	10
2	4	3	1	9	10	9	6	6	8	5	8

[1]Bud No. 1, apical bud pair; bud pair No. 3 developed erratically since many of the buds were submerged in water.

Data for three observation dates, on the basis of stage *c* development only, are shown in Table 3. These data indicate that the effects of GA and TIBA on aspen are similar to the effects on maple. GA not only brought about a more rapid break of dormancy, but also resulted in an obvious inhibition of the lateral buds below No. 1 which increased with increasing treatment concentration. Conversely, TIBA caused an increased development of the laterals lying below bud No. 1. This can be noted in the data for April 19, but because of the arbitrary classification scheme, it is no longer evident by April 30. However, visual observation revealed a marked difference among TIBA treatments both in aspen and maple at the later dates. Although the number of buds reaching stage *c* did not differ greatly among treatments, the lateral buds (or shoots) in the TIBA-treated cuttings for both species were much further advanced and larger than either the controls or the other treatments. The inhibition noted in maple was evident to only a slight degree in the lowermost buds of the IAA-treated aspen cuttings.

Bebb willow. Cuttings were collected from the 1-year-old branch shoots of a single, bushy tree on April 5, 1957. Eight lateral buds were retained on each cutting. Internodes averaged about one-half inch in length.

The first observations showed 21 out of 30 GA-treated apical buds in stage *a* on April 11, whereas all buds in the other treatments were still dormant. The number of apical buds which had broken dormancy by April 15 is shown in Table 1. One-hundred-percent apical bud burst occurred April 15 in the GA-treated cuttings but was never attained in either the TIBA- or IAA-treated cuttings; 27 out of 30 TIBA-treated and 24 out of 30 IAA-treated apical buds broke dormancy during the course of the test.

TABLE 3. Number of quaking aspen buds attaining stage c.

Date and bud No.[1]	Treatment										
	GA			TIBA			IAA				No
	¼%	½%	1%	¼%	½%	1%	¼%	½%	1%	Lanolin	lanolin
April 15											
No. 1	3	4	7	--	--	--	--	--	--	--	--
2	--	--	1	--	--	--	--	--	--	--	--
3	--	--	--	--	--	--	--	--	--	--	--
4	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--	--
April 19											
No. 1	10	10	10	10	10	10	9	10	9	10	5
2	6	5	8	10	8	9	7	7	7	7	7
3	5	3	2	10	8	8	6	7	7	8	4
4	2	--	--	4	5	7	4	4	2	7	5
5	2	1	--	4	6	3	1	1	1	4	4
2–5	15	9	10	28	27	27	18	19	17	26	20
April 30											
No. 1	10	10	10	10	10	10	10	10	10	10	9
2	7	7	9	10	10	9	10	10	10	10	10
3	9	4	4	10	8	9	8	10	10	10	9
4	4	3	--	9	7	8	5	6	7	9	9
5	5	3	--	6	10	5	3	4	4	7	6
2–5	25	17	13	35	35	31	26	30	31	36	34

[1]Bud No. 1, apical bud; bud No. 6, basal bud, developed erratically since many of the buds were submerged in water.

As in the other species, GA not only brought about a more rapid break of dormancy of the apical buds in willow, but also resulted in a very marked inhibition of lateral bud development. TIBA brought about a slightly earlier bud break, but did not affect the development of the lateral buds as noted in maple and aspen. IAA caused a very marked inhibition of apical bud development; the laterals developed somewhat better than those of the other treatments.

Winter Collection Results

The results of the second experiment, conducted in January 1958, were similar to the 1957 test: the GA-treated cuttings not only broke dormancy earlier but also attained a considerably higher percentage of total apical bud break than the controls. Exceptions were northern red oak, which showed no effect of GA treatment, and butternut, which showed only slight effects. In the oak the first break of dormancy occurred 34 days after treatment for both the treated and control cuttings. In the butternut the treated cuttings began breaking dormancy 25 days and the controls 46 days after treatment, but the total apical bud break was only 35 and 50 percent respectively.

Considering all species, the GA-treated juvenile cuttings broke dormancy earlier than similarly treated mature cuttings of the same species. But in comparison with their respective controls, the untreated juvenile cuttings usually broke dormancy within a few days of the treated, while in the mature cuttings this interval was extended to about 2 weeks.

Discussion

It is apparent that GA induced premature apical bud growth, as compared with the controls, in all three species. This conclusion is in general accord with the findings of the previously cited investigators who demonstrated that GA can overcome bud dormancy. The inhibition of the lateral buds, however, cannot be explained as a typical response. GA has been shown to have no inhibiting effect on lateral buds under most conditions (Kato, 1953; Bradley and Crane, 1957; Stowe and Yamaki, 1957), although Marth *et al.* (1956) did find that GA produced longer but fewer laterals on English boxwood. Furthermore, Brian and Grove (1957) noted that if the growing point of *Lathyrus odoratus* was excised, GA could not inhibit the growth of the laterals. But if the growing point were left intact and it ceased to elongate, then GA could cause it to resume growth and formation of laterals would be inhibited.

The normal course of bud break on short, woody cuttings tends to begin at the apex and is accompanied by some suppression of the underlying laterals, but not to the extent exhibited by the GA-treated cuttings in this study. Such a degree of lateral bud inhibition may presumably be explained as an indirect consequence of the GA treatment. Apical bud development was unquestionably stimulated by all concentrations of GA considerably in advance of the lateral buds lying below the point of GA application. The precocious development of these apical buds could in turn exert apical dominance over the laterals lying below them, thereby inhibiting any GA-stimulated growth.

Development of the laterals was also suppressed to a degree in the control groups, but much less than in the GA-treated cuttings. Furthermore, lateral bud inhibition increased slightly with increasing concentrations of GA in all three species. This phenomenon is difficult to explain on the basis of apical dominance alone, since no differences were noted in apical bud development among GA concentrations. Evidence recently presented indicates that GA acts additively when applied in combination with small quantities of IAA (Brian and Grove, 1957; Kato, 1958). In a similar manner, GA may conceivably react synergistically with the auxin produced by the apical bud in suppressing the laterals. Any interaction of GA and endogenous auxin would, in this case, tend to be accentuated by the site of application immediately above

the apical bud of the cutting.

The aforementioned GA-manifested responses are not confined to woody cuttings severed from the parent plant. In October 1957, prior to normal cold exposure, 33 quaking aspen root suckers were potted and brought into a warm greenhouse. On December 17, at which time none of the buds showed signs of breaking dormancy, they were decapitated and a 1-percent GA-lanolin paste was applied to the cut surfaces of 30 of the plants; the remaining 3 plants were decapitated, but untreated. By December 31, 2 weeks after treatment, 26 of the GA-treated plants had broken dormancy, and the remainder by January 6; the 3 control plants broke dormancy on April 7, 23, and May 10, 1958. Again, in the GA-treated plants, the apical bud broke dormancy first and in 9 of these plants the first lateral below the apical bud developed. Of the lower-lying laterals, only one developed within the 3-week observation period although 6 to 12 buds were retained on each plant.

It was recognized during the course of the experiment that cuttings collected in early April could not be considered in a state of true winter dormancy, since normal bud growth commences under natural conditions within a few weeks of this time. Under Doorenbos' (1953) classification scheme these cuttings would be considered in a state of "imposed dormancy," in which the buds have received sufficient cold exposure but remain inactive until induced to growth by favorable environmental conditions. In contrast, buds in a condition of true winter dormancy have not received the full period of cold exposure necessary to bring them into a state of "imposed dormancy."

This condition was demonstrated in the second experiment conducted during January 1958. Buds on many of the control cuttings failed to break dormancy during the 4-week period of the test. These results suggest that the cold exposure up to January 9 was insufficient to entirely overcome the true winter dormancy condition in most of the species tested. Nevertheless, GA was effective in eliciting active bud growth in a high percentage of the treated cuttings.

Observations have been made that GA does not induce formation of callus tissue on cut surfaces (Kato, 1953), although under certain conditions it may promote cambial activity in woody stems (Bradley and Crane, 1957). GA did not promote callus formation nor was there evidence of cambial stimulation on the short internodes projecting above the apical buds on any species included in the present study. The cut surfaces of the GA-treated cuttings maintained a "fresh" appearance, but this cannot be attributed to GA: the lanolin controls responded similarly.

Two other growth regulators were included in the experiment in order to compare the responses of a known auxin, IAA, and a known anti-auxin, TIBA, with those of GA. The temporary inhibition of bud development in the IAA-treated cuttings is a typical response to supra-optimal applications of this growth hormone. It has been established through numerous experiments that IAA may be substituted for the apical bud in dominating the growth of the laterals. No logical explanation can be offered for the apparent ineffectiveness of IAA on quaking aspen.

The TIBA-induced lateral bud development is, in general, consistent with the conclusions of previous investigators. TIBA has been shown to interfere with auxin translocation by inhibiting its normal polar movement through the stem (Hay, 1956; Niedergang-Kamien and Skoog, 1956; Niedergang-Kamien and Leopold, 1957). Vigorous lateral bud growth of the cuttings could therefore be attributed to the TIBA inhibition of, or interference with, the polar transport of endogenous auxin from the developing buds. This suppression of auxin movement, with the consequent elimination of apical dominance, would enable each lateral to break dormancy and elongate more or less independent of superior buds. Under certain conditions, GA has been found to completely counteract the inhibit-

ing effects of TIBA (Applegate, 1957). It is interesting to speculate as to whether GA would have a similar influence on the growth of the laterals of TIBA-treated woody cuttings.

The high concentrations of TIBA applied to the cuttings were not, however, conducive to continued growth even though the initial response of maple and aspen appeared favorable. At the end of the experiment (4 weeks after treatment), the internodes projecting above the apical buds on the TIBA-treated cuttings had turned black and died, and many of the apical shoots showed obvious signs of injury.

Summary and Conclusions

Gibberellic acid applied in concentrations of ¼, ½, and 1 percent in lanolin paste to dormant cuttings of red maple, quaking aspen, and Bebb willow induced preseasonal growth and development of the apical buds. It was believed that the precocious development of these buds indirectly suppressed the growth of the underlying laterals by exerting apical dominance over them. Increasing lateral bud inhibition with increasing GA concentration indicated an additional, unexplained direct effect. Similar concentrations of TIBA resulted in lateral bud growth comparable with that of the apical buds. This was believed due to the inhibition of endogenous auxin transport by TIBA and the negation of apical dominance. IAA, in the same concentrations, caused a temporary delay in bud break by exerting a simulated apical dominance over all buds on the cuttings.

It has been found that gibberellic acid can bring about a resumption of growth from different conditions of dormancy in many woody species. These findings may have potential application in forest research, where it is often desirable to promote the growth of dormant plants and cuttings or to prolong the normal growth period.

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Centenary Publications on Indian Forestry

The Government of India proposes to celebrate the centenary of forest administration in India during 1961 by issuing two volumes of centenary publications. These will describe India's forests in all their aspects. Included will be articles of general interest on forestry from eminent foresters in India and abroad. The President, Forest Research Institute and Colleges, Dehra Dun, U.P., India, will gratefully acknowledge contributions for the above publications.

Errata

In the article *Systematic Sampling with Multiple Random Starts* by Cherng-Jiann Shiue (*Forest Science* 6: 42-50) the following corrections should be noted.

Page	Column	Line	In Error	Corrected
44	left	12th from bottom	$= \frac{1}{NM-1}$	$= \frac{-1}{NM-1}$
44	right	4th from top	MS_b	MS^2_b
44	right	11th from top	S_b	S^2_b
44	right	9th from bottom	S_w	S^2_w
47	left	6th from bottom	S_w	S^2_w
47	right	Formula (10)	not clear	$\log M = \frac{1}{b}\left[\log S^2 - \log a - \log (1+b)\right]$

Asymmetric Distribution of a Substance Found in Horizontally Displaced Eastern White Pine Leaders which Reacts With Salkowski Reagent

BY
ARTHUR H. WESTING

AN AQUEOUS EXTRACT of the terminal shoots or leaders of eastern white pine (*Pinus strobus* L.) was found to change acidified ferric chloride from its normally pale yellow color to a reddish one. This reaction, first described by Salkowski in 1885, is characteristic of many indole compounds, occurring even when they are present in trace amounts. Indole compounds are, of course, of great physiological interest since several of them are auxins.

The distribution of the substance in the extract responsible for this reaction was investigated in connection with a study of the growth changes in a stem resulting from unilateral geotropic stimulation. When the stem of *Pinus strobus* or other conifer is displaced from its vertical orientation, the normal growth pattern becomes altered. The rate of growth of the cambium on the upper side decreases while that of the lower side increases. The wood that forms on the lower side of the stem is of an abnormal sort known as compression or reaction wood. The reader is referred to the article by Dadswell & Wardrop (1949) for a general description of this phenomenon.

The growth changes which occur when a stem is inclined suggest that a transverse asymmetry of auxin may be involved in the response. Indirect evidence of such an auxin gradient is found in the observation by Dadswell & Wardrop (1949) that in the spring cambial activity commences first on the lower side of leaning stems of gymnosperms. Nečesaný (1958) noted that cuttings made from the laterals of several conifers rooted more readily on their lower side, containing compression wood, than on the upper side.

The application of indoleacetic acid to conifer stems results in cambial stimulation and the formation of compression wood (Onaka, 1940; Wershing & Bailey, 1942; Fraser, 1952; Balch, 1952; Wardrop, 1957; Nečesaný, 1958). The question of whether horizontal displacement of a conifer stem results in a transverse auxin asymmetry was investigated by Onaka (1942). He reported that the lower cambial zone on inclined stems of *Pinus thunbergii* Parl. yielded two to four times as much diffusible

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This article is based on a portion of a dissertation presented for the Ph.D. degree in Yale University. The author gratefully acknowledges the guidance of his adviser Arthur W. Galston, Professor of Plant Physiology, Yale University. Thanks are also due Chester I. Bliss, Biometrician, Connecticut Agricultural Experiment Station, for assistance and George M. Furnival, Assistant Professor of Forest Mensuration, Yale Forestry School, for advice in the statistical analysis. The author is now with the Department of Forestry and Conservation, Purdue University, Lafayette, Ind. Manuscript received Aug. 8, 1959.

auxin as did the upper zone when the activity was tested in an *Avena* L. coleptile curvature test.

More recently, Nečesaný (1958) reported that ether extracts from the lower side of the laterals of *Pinus sylvestris* L. exhibit growth-promoting properties, while those from the upper side exhibit growth-inhibiting properties when tested in the straight-growth test utilizing excised *Triticum* L. coleoptiles.

Materials and Methods

Seedlings 8 to 12 years in age, averaging 280 cm in height, and having leaders averaging 50 cm in length were selected for vigor, straightness, vertical growth, and uniformity. They were chosen from among a natural stand of trees on an old field in the Yale Forest in Swanzey Township, New Hampshire.

The trees were subjected to one of three treatments for various durations. *Treatment A* consisted of bending a tree over so that its leader was displaced to a horizontal position. *Treatment B* was identical with Treatment A except that the apical 5 mm portion of the leader was excised and the leaves of the leader removed. *Treatment C* was identical with Treatment B except that an additional 5 mm portion was excised from the apical end of the leader at weekly intervals. Controls for each treatment were vertical trees either left intact or mutilated as indicated. The three treatments were initiated at weekly intervals from May 16 to July 4, 1958. On July 11 all leaders were excised and immediately placed into a portable freezer packed with solidified carbon dioxide and then kept frozen until used in the laboratory.

The mutilation of the leaders subjected to Treatments B and C considerably retarded their overall growth rate, the two treatments having morphologically indistinguishable effects. Under all three treatments the leaders exhibited growth depression on the upper side, growth promotion on the lower side, and they formed compression wood on the lower side.

The Salkowski-positive substance (SPS) responsible for turning the Salkowski reagent red was extracted by homogenizing a stem sample in sufficient 0.1 M KH_2PO_4 so that each milliliter of final extract represented 34 mg of original tissue. The homogenate was then centrifuged, the supernatant filtered through Whatman No. 5 paper, and the extract stored frozen until assayed.

Extracts were tested for their SPS content by a method modified from an assay for indoleacetic acid by Tang & Bonner (1947). One milliliter of extract was combined with 4 ml of Salkowski reagent[1] and the subsequent change in color intensity determined after 20 minutes with a photoelectric colorimeter equipped with a filter transmitting wavelengths 530 ± 30 mμ.

Experimental Results

The longitudinal distribution of SPS was examined in vertical control leaders as well as in horizontally displaced leaders. The results indicated a uniform distribution along the leader in each case.

Transverse distribution in the leaders was determined by splitting a leader longitudinally into upper and lower halves and comparing the SPS contents of extracts prepared from the two portions. A summary of the results of this investigation is presented in Table 1. The data were subjected to an analysis of variance, the results of which are summarized in Table 2. A transformation of the data to logarithmic units was necessary because the magnitude of the difference between upper and lower sides depended on the total amount of SPS.

The analysis demonstrated that inclination of the leaders resulted in a transverse asymmetry of SPS activity to the extent that about 60 percent of the total activity of a leader was found in the lower longitudinal half; this difference was found to be significant at the ½ percent level (Table 2, line 1). The redistribution occurred irre-

[1]Salkowski reagent: 0.5 M $FeCl_3 \cdot 6H_2O$ + H_2O + 17.8 M H_2SO_4, 3:100:60 by volume.

TABLE 1. Distribution of SPS in the leaders following horizontal displacement. In Treatment A *the leaders were left intact, in* B *they were defoliated and decapitated, while in* C *these decapitations were repeated periodically.*

Duration of treatment (weeks)	Average SPS Activity[1] (standard units)					
	Treatment A		Treatment B		Treatment C	
	Upper side	Lower side	Upper side	Lower side	Upper side	Lower side
0	107	120	....	....	....	....
1	107	143	110	140	127	127
2	100	183	110	150	73	110
3	93	130	87	147	80	80
4	143	193	100	87	70	97
5	110	157	63	73	33	47
6	107	130	40	50	17	33
7	87	137	33	67	30	47
8	103	123	33	40	50	47
			Vertical Controls			
3	....	....	50	47	53	47
6	....	....	43	47	70	80

[1]Each value is the average of 3 trees with the following exceptions: Treatment A, Duration 0: 6 trees; Treatment B, Duration 1: 2 trees; Treatment B, Duration 6: 2 trees.

TABLE 2. Analysis of variance of the distribution of SPS in the leaders.

	Degrees of freedom	Sum of squares	Mean square	F ratio	Probability
Difference between the logarithms of upper and lower sides					
1. Combined mean	1	11781	11781	37.28	0.005
2. Among treatments	2	218	109	0.34	.....
3. Among weeks	7	3237	462	1.46	.....
4. Treatments × weeks	14	6630	474	1.50	.....
5. Replicate trees	46[1]	14517	316		
Combined logarithms of upper and lower sides					
6. A vs. B and C	1	57800	57800	36.44	0.005
7. B vs. C	1	6325	6325	3.99	.....
8. Slope, combined	1	45048	45048	28.40	0.005
9. Slope, A vs. B and C	1	18113	18113	11.42	0.005
10. Slope, B vs. C	1	200	200	0.13	.....
11. Slope, scatter	18	22478	1249	0.79	.....
12. Replicate trees	46[1]	72952	1586		
13. Slope, A	1	160	160	0.10	.....
14. Slope, B and C	1	63001	63001	39.72	0.005

[1]Two degrees of freedom were lost because of 2 missing values for which best estimates were substituted.

spective of mutilation (Table 2, line 2) and it was not influenced by subsequent duration of treatment (Table 2, line 3).

The overall SPS content of a stem was uninfluenced by inclination (Table 2, line 13), but decapitation resulted in a decline (Table 2, line 14). This decline appears to be proportional, on a logarithmic scale, to the duration of the treatment since the linear terms account for all of the regression variance (Table 2, line 11). Although the SPS contents of decapitated leaders were significantly different from those left intact (Table 2, lines 6 and 9), activities of the leaders which had been decapitated repeatedly were not significantly different from those decapitated only once (Table 2, lines 7 and 10).

While Treatments B and C involved both decapitation and defoliation, it was determined from other experiments that the steady decline in SPS activity observed in these treatments was the result of the decapitation and not of the defoliation. It was further determined that this decline in SPS content could not be prevented by repeated applications of 0.5 percent α-naphthaleneacetic acid or 0.5 percent gibberellic acid in lanolin to the cut stump of the leader. The α-naphthaleneacetic acid did, however, prevent the transverse redistribution of the SPS.

Analyses made of material collected at different times in the growing season, revealed a steady overall decline of SPS in the leaders as the season progressed.

Preliminary Characterization

Extracts were found to retain their full chromogenic properties with Salkowski reagent even after 15 minutes of boiling. SPS also readily passed through dialysis tubing. The substance was further found to be almost completely soluble in methanol, but not in ether at pH values between 2.8 and 7.0.

The absorption spectrum from 350 to 750 mμ of an extract treated with Salkowski reagent was determined in order to compare it with several indole compounds similarly treated. The extract was found to absorb light from about 390 to 540 mμ with an indication of a peak at 405 mμ. The possibility exists, therefore, that the extract contained any of a number of indole compounds, but greater purification would be necessary for definitive results.

Another approach to the characterization of SPS was through the use of chromatography. An ascending method of paper chromatography[2] was modified from the ones described by Sen & Leopold (1954) and Stowe & Thimann (1954) for separating indole compounds. A reddish spot, presumably SPS, was observed at an R_F of 0.33.

Discussion

The acidified ferric chloride reaction was reported by its discoverer Salkowski (1885 a and b) to be specific for indoleacetic acid. Several dozen other indole compounds, however, have since been found to give positive reactions with Salkowski reagent (Tang & Bonner, 1947; Gordon & Weber, 1951; Sen & Leopold, 1954; Stowe & Thimann, 1954). About a dozen of these produce reddish colors, several having R_F values in the neighborhood of 0.33.

Very few non-indole compounds, on the other hand, have been reported that react with Salkowski reagent. Sen & Leopold (1954) reported blue colors for both indigo disulfonate and indigo tetrasulfonate. Of greater interest, Nichols (1958) reported a pink color for a probable leucoanthocyanin obtained from the fruit of *Musa* L. which had an R_F value similar to that of the putative SPS spot.

SPS is thus possibly an indole compound, but it is not indoleacetic acid for the following reasons. SPS is insoluble in ether at a low pH value, and its lower R_F value shows it to be a somewhat more polar compound. Indoleacetic acid and SPS also react differ-

[2]Solvent system: Isopropanol + 17.0 M ammonia water + water, 8:1:1 by volume. Spray reagent: 0.5 M $FeCl_3 \cdot 6H_2O$ + 11.6 M HCl, 1:25 by volume.

ently with Salkowski reagent, attaining maximum colors at different rates. Fransson (1953 and 1959) describes a substance obtained from *Pinus sylvestris* L. with growth-promoting properties that also is not indoleacetic acid. Fransson's auxin is, however, soluble in ether and therefore apparently not the same as SPS. The growth-promoting property of Nečesaný's (1958) extracts mentioned above cannot be attributed to SPS for the same reason.

Since SPS is possibly an auxin involved in the growth responses of conifers exposed to unilateral geotropic stimulation, further study of this compound is warranted. Attempts should be made to characterize the substance, to test it for possible growth-modifying properties, and to survey its possible occurrence in other species.

Summary

An uncharacterized substance which reacts with acidified ferric chloride, possibly an indole compound, but not indoleacetic acid, was discovered in aqueous extracts of the terminal shoots of *Pinus strobus* L. The maintenance of the overall level of this substance was found to be dependent upon the apical region of the leader, but not on its leaves. Neither application of α-naphthaleneacetic acid nor gibberellic acid was capable of substituting for the excised tip region in this respect. The total level of the substance diminished as the growing season advanced. The substance is of particular interest because unilateral geotropic stimulation resulted in its transverse redistribution, roughly 60 percent of the total being found in the lower horizontal half. While the redistribution also occurred in decapitated leaders, it was prevented when α-naphthaleneacetic acid was applied to such leaders.

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Manual of Vegetation Analysis

By S. A. Cain and G. M. del Oliveira Castro. Harper and Brothers, New York. 327 pp. $7.50.

Review by William W. Chilcote
Department of Botany and Plant Pathology
Oregon State College, Corvallis

The title of this book may be misleading, since it is not a manual in the true sense. Rather, it is a book which reviews some of the concepts and methods in vegetation description and analysis which have been found useful by different ecologists dealing with different kinds of vegetation.

The book was conceived and written while the senior author was assigned to the Technical Assistance Mission in Brazil in 1955-1956, and engaged in vegetation studies. Collaboration of the junior author developed through his long interest in Brazilian vegetation and association with the Servico Nacional del Malaria.

Of particular interest to the authors was the application of concepts and methods developed in the northern countries to the more complex Brazilian vegetation. Their experience gained through using these methods and some new ones, sparked the idea of writing a manual aimed at methods in the study of tropical vegetation. Cain points out, however, as the book developed, it extended considerably beyond the provincial cast originally intended.

The primary concern of the authors is to present effective methods in describing and analyzing vegetation itself and not to deal with the causal relations involved. It is their firm conviction that sound description of vegetation —as quantitative as possible—but at the same time compatible with time and purpose—forms concrete and enduring contributions to knowledge. On the other hand, ecological work done in the absence of adequate studies of vegetation itself has limited meaning.

With this goal in mind, the chapters develop logically from the broad approach of the floristic geographer to the more detailed methods involved in the analysis of more localized and highly organized vegetation units.

The phytosociological characteristics and viewpoints will appear somewhat classical to the forester but he will recognize familiar ideas clothed in different terminology. The included glossary is helpful in this respect.

Of especial interest will be the chapter describing the composition, structure, and development of the tropical rain forest, the one on dominance, and the section describing some of the ways various phytosociological characteristics have been combined from the standpoint of describing, characterizing, and comparing different vegetation units.

For those concerned with vegetation this book makes its greatest contribution in pulling together heretofore widely scattered methods and concepts used in vegetation studies, and evaluating them on terms of a wide variety of vegetation types—including the tropical vegetation of Brazil.

Relative Tolerance to Complete Inundation Of Fourteen Bottomland Tree Species

BY
JOHN F. HOSNER

STUDIES of regeneration and succession of bottomland hardwood trees often emphasize the effect of flooding upon regeneration. However, little information is available concerning the relative tolerance to complete inundation of the various bottomland hardwood tree species.

Putnam (1951) in discussing the floodplain forests of the Mississippi River, stated, "A few days' submergence while the tree is in leaf is fatal." He also stated in the same publication that "Only willow survives complete inundation during the growing season." Demaree (1932), in experiments with cypress seedlings submerged in Reelfoot Lake and the Lower St. Francis River, found all plants dead after two weeks of complete submergence. Brink (1954), on the basis of observations in the lower Fraser River Valley, stated that "Cold, swift water did little but delay the growth of most (Western) species; slow moving or stagnant water, on the other hand, caused the death of nearly all aerial vegetation after a day or two of flood." Boxelder (*Acer negundo* L.) was one of the species observed.

More recent tests have been made under laboratory conditions. Tests at the Southeastern Forest Experiment Station (1958) with yellow-poplar (*Liriodendron tulipifera* L.) showed that submergence during the dormant season had little or no effect, but tests made during the growing season indicated that three days of flooding adversely affected that species and at the end of 14 days only five per cent of the seedlings remained alive. Hosner (1958) in a preliminary test with six bottomland species showed that black willow (*Salix nigra* Marsh.) exhibited the greatest tolerance to inundation followed by green ash (*Fraxinus pennsylvanica* Marsh.), redgum (*Liquidambar styraciflua* L.), boxelder, eastern cottonwood (*Populus deltoides* Bartr.) and silver maple (*Acer saccharinum* L.) in that order.

Briscoe (1957) in submergence tests with northern red oak (*Quercus rubra* L.), cherrybark oak (*Q. falcata* var. *pagodaefolia* Ell.), slash pine (*Pinus elliottii* Engelm.), water tupelo (*Nyssa aquatica* L.), and swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.), found the tolerance to inundation to be strongly correlated with the frequency of flooding of the typical natural site of the species. Northern red oak showed the least tolerance to submersion and water tupelo and swamp tupelo showed the greatest tolerance to complete submergence. Briscoe (1957) also showed that tolerance of seedlings to complete inundation increased with the age of the seedling.

Floods in the bottomlands of the Mississippi River Valley during the growing season are common. Records for the Mississippi River at Cape Girardeau, Missouri, for the period 1897-1954 showed that flooding may occur in any month of the year, but is most frequent during April, May, and June — the early part of the

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growing season. Fifteen-year records (1939-1954), taken by the Illinois State Water Survey on the Big Muddy River at the Murphysboro, Illinois, gaging station showed that the river failed to reach flood stage in only two years.

Similar data for the Kaskaskia River taken at New Athens, Illinois, showed that it failed to exceed its banks in only three years. The average consecutive period that the river was out of its banks was 20 days at New Athens and 17 days at Murphysboro. Flooding of low lying sites also may occur through the impoundment of rainfall and local runoff even though the rivers do not exceed their banks.

The following study was made to determine the relative tolerance to complete inundation of 14 species of bottomland tree species. The species used were: silver maple, eastern cottonwood, boxelder, black willow, green ash, redgum, American elm (*Ulmus americana* L.), hackberry (*Celtis occidentalis* L.), red maple (*Acer rubrum* L.), cherrybark oak, pin oak (*Quercus palustris* Muenchh.), shumard oak (*Quercus shumardii* Buckl.), sycamore (*Platanus occidentalis* L.), and buttonbush (*Cephalanthus occidentalis* L.).

Probably the most important result of flooding is the reduction of available oxygen. The varying conditions of natural flooding such as temperature, water movement, flora and fauna affect the oxygen supply. As the oxygen conditions change, the absolute number of days a particular tree could be expected to live might vary considerably, but the relative survival periods of the different species should not change appreciably. Thus, the relative tolerance rather than the absolute tolerance is more important in understanding the significance of flooding in the ecology of bottomland forests.

Procedures

The trees used in this test were current year seedlings grown from seed. The seeds of all species were collected in Southern Illinois except redgum and hackberry, which were purchased and the seed source unknown.

The seed was sowed directly into seven-inch unglazed clay pots containing a silt loam soil. Enough seed was placed in each pot to ensure at least five approximately uniform and vigorous seedlings per pot. The excess seedlings were removed prior to the test. The seedlings were allowed to develop well past the cotyledon stage prior to the initiation of the test. The actual height among species varied (Table 1) as the seed was sown at the time it became available or, in the case of fall-seeded species, as the weather became conducive to germination. Thus, at the time of the test, the sizes of the different species probably closely approximated the differences one would observe among the same species under natural conditions.

Testing consisted of determining the ability of the various species to withstand complete inundation for periods of 5, 10, 20, and 30 days. In addition, pots similar in all respects were kept as a check. Three water tanks that could be filled to a depth of 24 inches of water were used, each tank representing one replication for a total of three replications. Assignment of pots to a tank and within a tank was done in a random manner. At the beginning of the test the tanks were filled with tapwater. In addition, since floodwaters are often quite turbid, an attempt was made roughly to approximate commonly observed field conditions by adding enough silt and clay to the container to bring the turbidity of the water to more than 200 units of turbidity per thousand. Due to evaporative losses it was necessary on two occasions to add additional tapwater to the containers to keep the tallest trees completely submerged. The only agitation of the water occurred as seedlings were removed or additional water was added to the tanks.

All species of seedlings except redgum were placed in the tanks at the same time. The redgum was added later as room in the tanks became available. Each treatment and check consisted of three replications of five seedlings each for a total of 15 seed-

lings per treatment. The tanks were kept in a partially shaded greenhouse throughout the test and minimum and maximum water temperatures were taken every other day. As the seedlings were removed from the tank at the appropriate time intervals, they were placed on partially shaded greenhouse benches with the check plants. The inundation test began July 2 and ended August 1, 1958. Observations on all test trees continued until October 1, 1958.

Results

The results of the study show that under the conditions of the test there is considerable variation in the ability of bottomland tree species to withstand complete submergence. Only two cherrybark oak, one hackberry, and one redgum seedling died after five days of complete inundation. All seedlings of silver maple and buttonbush survived 30 days of complete submergence. In between these extremes a wide range of effects were exhibited by the various species. Some boxelder, willow, cottonwood, and ash also survived 30 days of submergence (Fig. 1).

The greatest increase in seedling mortality occurred between the 10- and 20-day series. At least one seedling of all species survived 10 days' submergence, whereas no seedlings of hackberry, red maple, shumard oak, redgum, or cherrybark oak survived 20 days. Only a few pin oak and elm survived the 20-day period and none survived 30 days.

Growth of all submerged seedlings was severely retarded (Figures 2, 3). No height growth occurred while the seedlings were submerged.

The results from the three replications were quite uniform although the seedlings in one replication where water temperatures were consistently one to two degrees lower than the other two showed slightly more tolerance to the submerged conditions.

For each species the number of surviving seedlings and the rate of recovery are indicated in Table 1. Recovery rates are relative among species subjected to the same treatment.

All check trees remained alive and vigorous throughout the entire period of observations.

Discussion

Many factors such as temperature, amount of water movement, chemicals, and organic matter in water, microbes, algae growth, soil characteristics and the like, would be expected to affect the length of time that

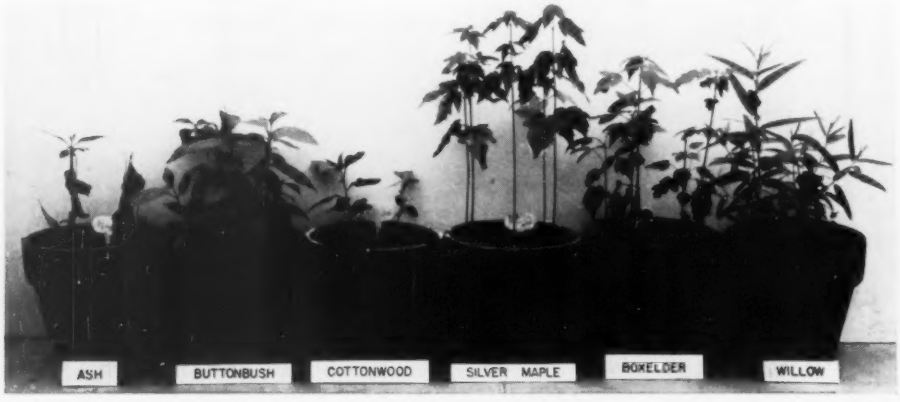

FIGURE 1. *Species surviving 30 days of complete inundation. Photograph taken 20 days after completion of submergence test.*

TABLE 1. Original seedling heights and subsequent survival of 14 species of trees subjected to complete inundation for four time periods.

Species	Initial mean hgt.	Number of days 5	10	20	30
	Inches[1]	*Number of surviving trees*[2]			
Silver maple	1.24	15 lived; recovered rapidly.	15 lived; recovered rapidly.	15 lived; recovered rapidly.	15 lived; 2 lost terminals; recovered rapidly.
Buttonbush	5.0	15 lived; recovered rapidly.	15 lived; recovered rapidly.	15 lived; recovered rapidly.	15 lived; 2 lost terminals; recovered rapidly.
Boxelder	6.5	15 lived; recovered rapidly.	15 lived; recovered rapidly.	15 lived; made medium recovery.	14 lived; 4 lost terminals; living trees made medium recovery.
Black willow	3.2	15 lived; no apparent effects.	15 lived; no apparent effects.	15 lived; recovered rapidly.	13 lived; 3 lost terminals; living trees recovered rapidly.
Cottonwood	2.8	15 lived; no apparent effects.	14 lived; recovered rapidly.	11 lived; 2 lost terminals; recovered slowly.	7 lived; 2 lost terminals; recovered slowly.
Green ash	7.4	15 lived; no apparent effects.	14 lived; recovered rapidly.	11 lived; 3 lost terminals; living trees made medium recovery.	3 lived; 2 lost terminals; recovered slowly.
American elm	9.1	15 lived; 14 trees developed side branches; recovered rapidly.	15 lived; 7 lost terminals; recovered rapidly.	4 lived; all terminal shoots died; living trees sprouted weakly.	none
Pin oak	5.8	15 lived; recovered rapidly.	14 lived; living trees recovered slowly.	4 lived; living plants recovered very slowly.	none
Sycamore	4.6	15 lived; recovered rapidly.	15 lived; some made medium recovery.	none	none
Red maple	3.9	15 lived; recovered rapidly.	14 lived; made medium recovery.	none	none
Shumard oak	5.2	15 lived; only 2 plants grew in height after flooding.	14 lived; recovered slowly.	none	none
Redgum[3]		14 lived; 4 lost terminals; recovered rapidly.	10 lived; living trees made medium recovery.	none	none
Hackberry	8.6	14 lived; 4 lost terminals; recovered slowly.	1 lived; developed as weak sprout.	none	none
Cherrybark oak	5.5	13 lived; living trees made medium recovery.	1 lived; recovered very slowly.	none	none

[1]Based upon the measurement of 15 individual seedlings.
[2]Based upon a total of 15 seedlings per treatment.
[3]Tested separately but under similar conditions. Heights were not measured.

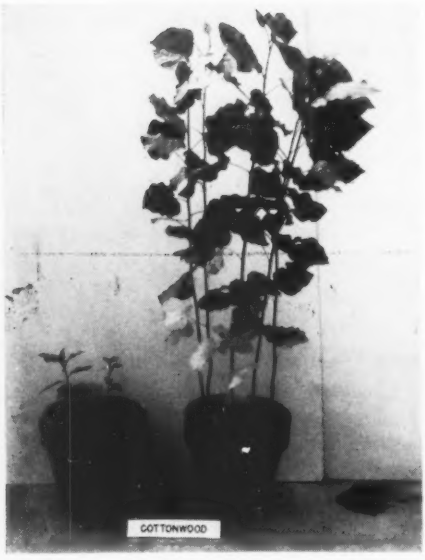

FIGURE 2. *Left: Cottonwood seedlings inundated 30 days. The inundated seedlings, removed from the water 20 days prior to the time of the photograph, recovered slowly. Right: Check seedlings.*

seedlings will withstand complete submergence. The mean maximum and mean minimum temperatures were 83°F and 78°F. In no case did an individual measurement vary by more than three degrees from the mean. A heavy growth of algae appeared on the water surface of all tanks, culminating approximately two weeks after the initiation of the test.

Turbidity, as measured with a Jackson turbidimeter according to procedures described by the American Public Health Association (1955), dropped to less than 25 units per thousand the third day after the initiation of the test and remained less for the remaining submergence period. The water at 25 units of turbidity was clear enough to permit easy identification of the submerged seedlings.

The outstanding survival of silver maple was in contrast to the earlier results of Hosner (1958). However, the maple seedlings in the earlier test showed a lack of vigor originally which may have caused the poor survival. Part of the success of silver maple may also be due to their original greater height (Table 1), which resulted in the crown being nearer the surface of the water where oxygen levels probably were higher. Since tree seedlings can withstand saturated soil conditions much longer than complete inundation lack of oxygen available to the tops is a critical factor in survival. In some cases the species tolerances to flooding as brought out by this test did not correspond exactly to the sites on which

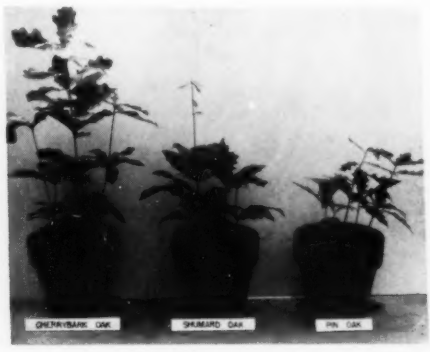

FIGURE 3. *Left: Oak seedlings submerged 10 days. Photograph taken 40 days after seedlings removed from water. Right: Check seedlings.*

the species are found under field conditions. Both Hosner (1957) and McDermott (1954) list red maple as a wet site tree but it exhibited less tolerance to flooding than silver maple which is usually associated with better drained sites. The red maple seeds used in the study were collected from upland trees. Perhaps seed from trees naturally growing in a poorly drained area may have given different results. The same general explanation also may explain why redgum failed to tolerate longer submersion periods. The seed was purchased and no information was available to indicate whether the seed was collected from trees growing in the uplands or in the bottoms. Redgum, although not a true swamp species, is often found on poorly drained bottomland sites with pin oak and American elm.

Both cottonwood and silver maple are usually associated with better drained areas yet both were very tolerant to submersion. Apparently there are other factors such as seedbed conditions and ground cover which may control the establishment of flood tolerant silver maple and cottonwood and limit their appearance on the more poorly drained sites.

Conclusions

This study shows that under the conditions of the test there is considerable variation in the ability of different bottomland species to withstand complete submergence. For the species tested these relative tolerances to complete inundation indicate a definite range from most to least tolerant as follows: silver maple, buttonbush, boxelder, black willow, cottonwood, green ash, American elm, pin oak, sycamore, red maple, shumard oak, redgum, hackberry, and cherrybark oak.

Thus, it seems reasonable to assume that high water in some bottomland areas exercises a selective killing effect on reproduction and thereby affects the makeup of individual stands. However, many species exhibit a greater or lesser tolerance to flooding than species-site relationships indicate. This means that other factors also play an important part in determining the regeneration and succession of tree species in bottomland hardwoods. Water apparently is most likely to become the limiting factor only on sites that are consistently flooded for fairly long periods of time during the growing season, such as true swamps, deep sloughs, and backwater areas.

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The Oaks

Die Eichen (The Oaks) by Joachim Krahl-Urban. 288 pp., 110 illus. Paul Parey, Hamburg and Berlin, 1959 [In German.] 48 DM.

Review by Paul O. Rudolf
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Forest Service, U. S. Department of Agriculture

English oak (*Quercus robur* L. or *Q. pedunculata* Ehrh.) and durmast oak (*Q. petraea* (Matt.) Liebl. or *Q. sessiliflora* Salisb.) are the common oaks over much of Europe, although the former has the more extensive range. They are both white oaks. Their importance in present European forests lies not so much in their abundance, which is small compared to that of pine, spruce, and beech, for example, but in the high value of products, such as veneer logs, they can produce and their ecological significance.

A voluminous literature has developed concerning these oaks, and the author has done a real service in sorting out and welding the most significant items into a comprehensive and reasonably compact monograph. This the author is well qualified to do. He has worked with and studied these oaks for some 30 years in Germany and has made special trips to study them throughout a major part of their European ranges. Results of his own research and experience are a part of the book and helped him to evaluate the reports and findings of others.

The book is logically arranged into five sections, each with two or more chapters. The first two sections are introductory and cover the present and past distribution of the oaks, their importance from prehistoric to present times, and the uses of the wood, bark, foliage and acorns. The third section covers primarily botanical descriptions of the species, their variation, and hybridization; their silvical characteristics and requirements; and their major enemies. The fourth section is the heart of the book. It covers the whole range of silviculture and includes discussions of silvicultural systems (high forest, coppice, and coppice-with-standards), pure and mixed stands, timber stand improvement activities, stand establishment (natural and artificial regeneration), and seed and nursery practices. The fifth section concerns chiefly the production and selling of oak timber. It includes specifications for various types of products.

The secton on silviculture is most complete and will undoubtedly be of greatest interest to most readers. It stresses the value of mixed stands (and compares various mixtures) for growing the large veneer-quality trees that are the premium product of oak in Germany. Throughout this section the author brings in frequent examples from his own experience and research. His strong interest in provenience studies makes itself evident and adds much to the value of the book.

Although a few photographs leave something to be desired, the book on the whole is very well illustrated. In addition to numerous photographs there are several helpful graphs and charts and a number of useful tables. An especially valuable feature of "Die Eichen" is a list of 782 references relating to durmast and English oaks arranged by the following countries of origin: Germany, Austria, and Switzerland combined (483 references); Belgium, Bulgaria, Czechoslovakia, Denmark, England, France, Hungary, Italy, Norway, Poland, Rumania, Russia, Sweden, Turkey, United States, and Yugoslavia.

"Die Eichen" ought to be a very useful working tool for many European foresters and a "must" for those who are managing English oak or durmast oak stands. Because of a dearth of information on oak silviculture it would also make profitable reading for those American foresters who must manage white oak forests and can handle the German language.

The Biology and Ecology of the Red-Pine Sawfly in Wisconsin

BY
JOSEPH E. KAPLER
DANIEL M. BENJAMIN

THE RED-PINE sawfly (*Neodiprion nanulus nanulus* Schedl) is an important native defoliator of red and jack pine. Abundant in parts of Canada and the northeastern United States, it is common in Wisconsin, where it is a serious threat to the successful development of red pine forests.

Red pine (*Pinus resinosa* Ait.) is the predominant conifer being planted in Wisconsin at present. Between 1955 and 1957, nearly 55 million seedlings were distributed and by 1956 over 224 thousand acres had been planted. Establishment of red pine in pure stands has favored the increase of the red-pine sawfly. The investigation herein reported was undertaken to provide the biological and ecological information necessary should control operations be required in the future.

Distribution and Host List

The red-pine sawfly is nearctic in distribution; its range extends across northern North America. It feeds on red pine and on the only two species whose ranges overlap to form an east-west continental bridge: jack pine (*P. banksiana* Lamb.) and lodgepole pine (*P. contorta* Dougl.). Ross (1955) designated the eastern and western sawfly populations as subspecies. According to existing records, the two populations are separated by a gap extending from western Alberta to Saskatchewan. Figure 1 shows the eastern population distribution. Red pine and jack pine are the two most common hosts of the eastern population, with the former being preferred. Craighead (1949) reported this sawfly on Japanese red pine (*P. densiflora* Sieb and Zucc.) and Swiss mountain pine (*P. mugho* Turra). The western population occurring in Oregon, Idaho and Alberta feeds on lodgepole pine.

FIGURE 1. *Distribution of red-pine sawfly in North America.*

The authors are respectively Assistant Professor of Biology, Loras College, Dubuque, Iowa, and Associate Professor of Entomology, University of Wisconsin, Madison.

A condensation of a thesis submitted in partial fulfillment of the requirements for the Ph.D. degree, University of Wisconsin. Studies financed jointly by the Wisconsin Alumni Research Foundation, the Wisconsin Conservation Department and the University of Wisconsin. Approved for publication by the Director of the Wisconsin Agricultural Experiment Station, March 7, 1959. Manuscript received Sept. 28, 1959.

First reported in Wood County, Wisconsin, in 1946, the red-pine sawfly has been common throughout the state in recent years. It is present generally wherever red pine stands occur. Red pine grows naturally in the northern two-thirds of the state, and has been planted south to the Illinois border.

The heaviest known infestation during the period of investigation was in a 33-acre, red pine and eastern white pine (*Pinus strobus* L.) plantation at the State Game Farm near Poynette in Columbia County. The stand is in excellent condition, the trees are vigorous, and growth has been rapid. The canopy is closed, shading out all ground vegetation. The litter consists of fallen needles, leaves and pruned branches. Observed initially in 1952, severe defoliation occurred in 1955 and 1956, but declined in 1957.

A light red-pine sawfly infestation in the red pine plantations in the University Arboretum in Dane County observed in 1954 now appears more abundant than in previous years. The red pine is from 4 to 20 years old, and occurs in both open and closed stands. The studies herein reported were conducted chiefly at these two sites.

Taxonomic Position

The first reference to the red-pine sawfly was in a report by Schedl (1931) on *Neodiprion* sawflies attacking jack pine in Ontario in which he designated this undescribed species as the "black-headed jack-pine sawfly." The name *nanulus* appeared in a paper discussing the application of Dyar's rule (Schedl, 1933). Schedl (1935) formally described *N. nanulus*, using specimens collected at Biscotasing, Ontario, as holotypes. Further field and population dynamics studies on the sawfly in Ontario were published by Schedl (1937 and 1938).

Atwood and Peck (1943) reported taxonomic studies of the red-pine sawfly and others of the genus *Neodiprion* in Canada. This report included keys to the female adults and larval forms of the native species attacking pines. Ross (1951) placed *N. nanulus* Schedl in the "Abietis" group in the check list of Hymenoptera of America north of Mexico. He designated *N. nanulus contortae* Schedl as the western subspecies and *N. nanulus nanulus* Schedl as the eastern subspecies (Ross, 1955). He further postulated that the latter species evolved in the West and spread to the East so recently that there has been no opportunity for its isolation and evolution into a distinct species.

FIGURE 2. *Adult female (left), and male (right) red-pine sawfly.*

Descriptions of Stages

Adults. The adult female (Fig. 2) has an average length of 7.3 mm, with a range from 6.6 to 8.0 mm, based upon measurements from 50 specimens collected at Poynette. In general, the body is yellowish brown, with the exception of a dark brown to black metanotum and metascutellum. These dark areas, however, are not readily observed when the wings are folded in a resting position. The legs are the same color as the body. The wings are vitreous and opalescent with dark venation. The antennae are 20 to 21 segmented. The antennae, compound eyes and ocelli are dark brown to black, and contrast with the yellowish-brown head.

The adult male is smaller than the female and averages 5.7 mm, with a range from 5.0 to 6.3 mm (Fig. 2). The body

is black, excepting the abdominal sternites, which are reddish brown. The legs are yellowish brown. The bipectinate, black antennae are 24 to 25 segmented.

Eggs. The egg is oval and slightly flattened on the dorsal side, light green, with a smooth translucent chorion. Measurements made by Brygider (1952) are as follows: Length—1.72 mm, thickness—0.43 mm, and width—0.23 mm.

Larvae. Male red-pine sawfly larvae pass through four feeding instars and the females five.[1] The bodies of the first three are pale grayish green with a shiny black head. The third instar has dark longitudinal markings, and the fourth instar clearly shows these dark stripes along the length of the body. The fifth instar is approximately 19 to 22 mm long (Fig. 3). On each side of the mid-dorsal line is a narrow dark stripe. Lateral to this is a more prominent dark supraspiracular stripe which extends from the prothorax to the epiproct. Below the supraspiracular stripe is a pale spiracular stripe. A dark band extends from the first to the eighth abdominal segment at the base of the prolegs. The dorsal surface is olive green in contrast to the light greenish white ventral surface. The thoracic legs are black with whitish annulations.

[1]Personal communication, D. R. Wallace, Sault Ste. Marie, Ontario, Canada.

FIGURE 3. *Fifth instar larva of red-pine sawfly.*

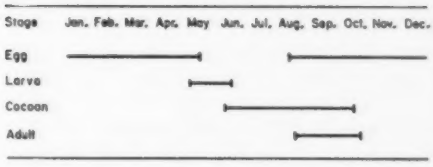

FIGURE 4. *Seasonal history of the red-pine sawfly in southern Wisconsin.*

The larvae molt once after feeding is completed. They become dull green on the dorsal surface and pale on the ventral side. The dark supraspiracular stripe is prominent, but the narrow dark stripes on each side of the mid-dorsal line are not as distinct. The head capsule is a dull yellowish brown.

Cocoons. The cocoons are tough, papery cylinders with rounded ends. Cocoons containing female larvae are larger than those containing males, and averaged 8.2 by 3.8 mm (50 measurements), while those of the males averaged 6.6 by 3.1 mm. Light colored when first formed, the cocoons turn golden brown and darken after a few weeks in the forest litter. Little deterioration of the cocoon occurs during the first year. Thus, it is often difficult to distinguish old cocoons from those of the current season.

Life History and Biology

Seasonal history. The red-pine sawfly overwinters as an egg in the needles of the host tree (Fig. 4). The larvae emerge during May and begin to feed on the needles in which the eggs were laid. They complete four or five feeding instars in 4 to 6 weeks. The prepupal larvae pass the summer in cocoons which are spun in the litter underneath the trees. Pupation occurs shortly before adult emergence, beginning late in August and extending into October. There is one generation annually although occasionally a small percentage of the prepupal larvae remain in diapause in their cocoons

for one or more years.

Adult emergence. Adult sawflies escape from cocoons as described for *N. lecontei* (Fitch) by Benjamin (1955). The adult uses the mandibles in a pliers-like action to cut an opening as it rotates within the cocoon. The sawfly emergence holes can be distinguished easily from those caused by parasites and predators by their larger size and smooth uniform contour on the ends of the cocoons.

The period of adult emergence is considerably longer than the period of larval emergence in spring. Adults appear in late August, and continue to emerge until about mid-October. At the University Arboretum and the Poynette Game Farm in 1955, 1956 and 1957, the peak of emergence was during the last two weeks of September.

Sex ratio. The sex ratio of the sawfly in Wisconsin averaged 58.2 percent females and 41.8 percent males from a sample of 3456 adults reared from larval collections made from 1955 to 1957.

Mating activities. Mating occurs shortly after the adults emerge. The female usually assumes a premating position near the end of a needle with her abdomen toward its tip. The males are very active in searching for a mate, and possess a remarkable ability to detect the presence of virgin females. Mating is accomplished while the sawflies face in opposite directions.

Fecundity. The eggs are fully developed and ready for fertilization when the female emerges from the cocoon. The fecundity was determined by counting the eggs in virgin females reared from cocoons collected at Poynette, and by counting eggs laid and those remaining in females after oviposition. Both caged adults and field-collected adults were utilized in obtaining information on fecundity.

The average number of eggs contained in 100 females before oviposition was 51.6 $\pm$ 8.3, with a range of 24 to 68. The average number of eggs retained by females after oviposition on red pine and jack pine was 2.5 and 1.5 respectively, with an overall average of 2.3 from 130 dissected females. The average was raised considerably by a few females containing 10 to 20 eggs, as 94 of the 130 females contained two or less.

Oviposition. Oviposition begins soon after mating. The outermost current year's twigs where large needles occur are usually selected. In open plantations, oviposition is in needles at the ends and outer one third of the twigs from the ground level to the leader, but more frequently on the twigs in the upper crown. No preference is shown for the exposed or the shaded side. It appears that site selection is mainly dependent upon needle condition, and not upon any specific location on the tree. In only one case was oviposition observed in two-year-old needles.

In selecting a needle for oviposition, the female begins at the base of the needle, and while palpating with her antennae, walks out to the tip. If the needle is unsuitable, she turns around and returns to the base of the needle, then moves out on another needle. This procedure is repeated until an acceptable needle is found, then the female crawls out to the tip or only part way, and then backs down toward the base to begin oviposition (Fig. 5).

One or two test cuts are usually made before an egg pocket is made to hold the first egg. Of 441 needles examined, 69 percent had these cuts. Invariably they are deeper than the egg pockets. This procedure may be a means of testing the suitability of the needle for oviposition.

Oviposition is accomplished in the same manner as with other *Neodiprion* sawflies. The opening is made at the edge of the needle, slightly to the flat side. The lancets are moved back and forth alternately as the ovipositor is moved forward until the egg pocket is formed. The ovipositor is retracted through the pocket as the egg is deposited. The egg lies just under the curved surface of the needle. After an egg is deposited, the female moves forward and be-

FIGURE 5. *Female red-pine sawfly depositing egg in pocket.*

gins to cut the next pocket. The eggs are laid singly in a row in the edge of the needle. The pockets are separated by approximately their own length (Fig. 5); however, the distance between slits frequently is less than their length. Most of the eggs from one female are laid on one twig. If the female is disturbed, or if the needles are unsuitable, she may move to another branch. After oviposition is completed, the female crawls to the base of the needle, and usually remains facing the twig until death occurs. Males are present among the trees for some time after all females have disappeared.

If mating does not occur within a few days after emergence, the virgin female will oviposit. All the progeny developed from unfertilized eggs are males; arrhenotoky is characteristic in *Neodiprion* sawflies.

From 4 to 13 eggs per needle were most common, and 9 eggs occurred most frequently; the mean was 8.5 eggs per needle. From 10 to 15 eggs per needle were reported as most common on red pine and three to eight on jack pine in Canada (Atwood and Peck, 1943). Schedl (1937) reported similarly for jack pine.

The distribution of eggs per twig from 200 field collections shows the 51 to 60 group as the most frequent, and 62 eggs per twig as the mean number (Fig. 6). The average number of eggs per female is 51.6 ± 8.3. This indicates that the female will usually oviposit her entire egg complement on one twig, as approximately 95.6 percent of the egg complement is laid. Limited studies with caged red-pine sawfly adults on jack pine in the University Arboretum indicate that they readily deposit all the eggs on one twig.

Twigs in the upper crown of closed stands generally contain greater numbers of eggs than twigs in the lower crown. In a closed stand, the females upon emerging will move up toward the light, resulting in a concentration of adults at the upper crown level. Oviposition usually occurs in the more luxuriant foliage at the tops of trees. Females are not strong fliers and do not move far after emerging if foliage is acceptable for oviposition. As a result, in heavy infestations, more than one female may oviposit in a single twig. As in open-grown trees, selection of the oviposition site

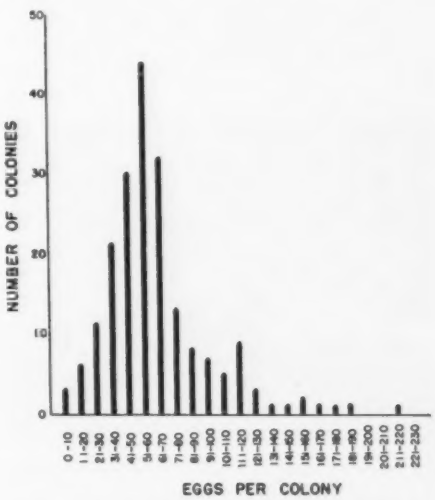

FIGURE 6. *Distribution of eggs per colony in red pine.*

seems to depend on the condition of the needles. Schedl (1938) reported a tendency for the red-pine sawfly to oviposit in shaded places, but this has not been observed in Wisconsin.

The heavy defoliation in 1955 and 1956 at Poynett resulted in reduced height growth and needle development of the infested trees in 1956. The 1956 needles on trees defoliated in 1955 appeared shorter and thinner than on normal trees and not as suitable for oviposition as were those in trees not so severely defoliated. Infestation in 1957 was heavier around the fringes of the previously heavily infested area, indicating that the females moved outward for oviposition. This resulted in a dispersal of the insect populuation. If this dispersal is the result of unsuitable foliage in severely infested trees, it may be an important factor in allowing the trees to recover after 2 to 3 years of heavy defoliation.

Larval feeding habits. Red-pine sawfly larvae feed only on old needles. First instar larvae crawl to the tip of the needle in which the eggs from which they have emerged were placed and begin feeding. They assemble in a ring about the needle, with their heads toward its tip (Fig. 7), as is characteristic of related species. Feeding begins at the tip and progresses down to the base. The

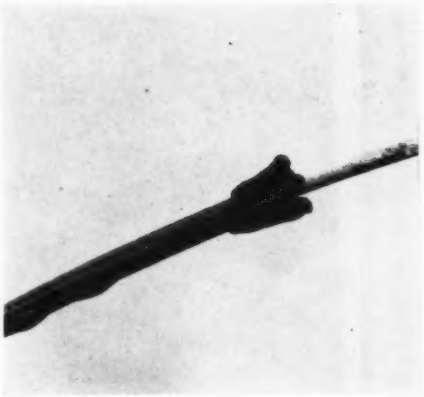

FIGURE 7. *First instar red-pine sawfly larvae.*

first and second instar larvae do not consume the entire needle, but feed only on the green outer layers of tissue, leaving a thin fibrous strand. This core soon dries and wilts, giving a tattered, straw-like appearance to the needles. The third instar, and some late second instar larvae, begin to consume the entire needle, but leave a persistent stub from ¾ to 1¼ inches long on red pine (Fig. 8). On jack pine, the stub is ¼ to ½ inch long. Feeding damage of the red-pine sawflly can be distinguished readily from that of *N. lecontei*, *N. pratti banksianae* (Roh.) and *N. sertifer* (Geoff.). These latter species leave no stub, but consume the entire needle down to the sheath, which eventually falls from the twig.

The larvae are gregarious throughout most of the feeding period. During the fourth instar they begin to disperse, especially if more than one colony is on a small branch. They consume all the old foliage on one branch before moving to another.

The larvae exhibit a characteristic reaction when disturbed. The head and thorax are reared back and the end of the abdomen is raised slightly; the larvae remain attached to the needle by their prolegs. This response is generally performed in unison by the entire colony. If the disturbance is continuous, the larvae will crawl down to the twig and hide among the bases

FIGURE 8. *Defoliation by red-pine sawfly larvae. Note characteristic shriveled needles of first and second instar feeding and stubs remaining of other needles.*

of the needles. Late fifth instar larvae drop readily from the trees at the slightest disturbance.

Cocooning. After feeding is completed, the mature larvae molt and drop to the ground. They spin their cocoons in the litter above the mineral soil. The larvae may crawl for some distance searching for a cocooning site, but usually spin under the trees on which they fed. Occasionally a cocoon will be spun on a branch of the tree.

Ecology

Phenology of larval emergence and development. Brygider (1952) described the embryonic development of the red-pine sawfly eggs as they enter winter diapause. The winter is passed as a well developed embryo. The egg maintains its original shape during the winter diapause, and noticeable swelling does not occur until shortly before hatching in spring. The period during which larvae emerge is relatively short. Emergence is completed within 3 to 4 days in the first half of May in southern Wisconsin, unless cold weather prevails, coinciding with the time hardwood leaves are just becoming green. The following list of phenological events occurring during development in 1956 and 1957 was compiled at the University Arboretum and at the Poynette Game Farm.

1. Larval emergence and early first instar.
   (a) Wild plum (*Prunus americana* Marsh.) in full bloom.
   (b) Leaf buds on oaks fully opened and staminate flowers well-developed. (*Quercus macrocarpa* Michx., *Q. alba* L., *Q. ellipsoidalis* E. J. Hill, *Q. velutina* Lam., *Q. rubra* L.)
   (c) Bigtooth aspen (*Populus grandidentata* Michx.) leaf buds opening.
   (d) Quaking aspen (*P. tremuloides* Michx.) leaves up to ¾ full size.
   (e) Staminate cones appearing on red pine (*Pinus resinosa* Ait.)
   (f) White spruce (*Picea glauca* (Moench) Voss) buds just beginning to open.
   (g) Pin cherry (*Prunus pennsylvanica* L.f.) in full bloom.
   (h) Trillium (*Trillium grandiflorum* (Michx.) Salisb.) beginning to bloom.
2. Second instar.
   (a) Jack pine (*P. banksiana* Lamb.) pollinating.
   (b) Choke cherry (*P. virginiana* L.) in bloom.
   (c) Trillium (*T. grandiflorum* (Michx.) Salisb.) in full bloom.
3. Third instar.
   (a) Red pine (*P. resinosa* Ait.) pollinating.
   (b) Black cherry (*P. serotina* Ehrh.) in full bloom.
   (c) Bridal wreath (*Spiraea van Houttei* (Briot) Zabel) in bloom.
4. Fourth and fifth instars.
   (a) Black locust (*Robinia pseudoacacia* L.) in bloom.
5. Completion of larval feeding.
   (a) New needles of red pine (*P. resinosa* Ait.) approximately 1 to 1½ inches in length.

Larval development in relation to temperature. Temperature accumulation is useful in determining the time of emergence and larval development. In this study, sawfly emergence and growth were observed in the University Arboretum and the air temperature data were obtained from the Truax Field weather station in Madison, 8 miles away. Air temperature influences the rate of egg and larval development as these stages are spent entirely in and on the needles of the host tree. The larval feeding period was used to calculate the base temperature, as emergence and development of the larvae could be readily observed.

Development in relation to temperature is expressed as a constant in the equation $k = y\ (t\text{-}a)$. In this equation y is the number of days required to complete development; t is the average daily mean temperature, and a is the base temperature. Using developmental data for 1956 and 1957, the base temperature a can be calculated by simultaneously solving the equations. Larval development required 29 days in 1956, and the mean daily temperature during this time was 63.9° F. In 1957 larval development required 41 days with a mean daily

temperature of 57.1° F. The two equations are solved simultaneously:

$$1956\ 29(63.9 - a) = 1853.1 - 29a$$
$$1957\ 41(57.1 - a) = 2341.1 - 41a$$
$$a = 40.7$$

Substituting the value for a in the equation for either year, the day-degrees required to complete larval development can be calculated:

$$1956\ k = 29(63.9 - 40.7) = 672.8 \text{ day-degrees}$$

and this solution can be checked by substituting in the equation for the other year:

$$1957\ k = 41(57.1 - 40.7) = 672.4 \text{ day degrees.}$$

The measured day-degrees, the summation of the daily mean temperature above the threshold of 40.7 degrees, is shown in Table 1 for the periods of larval emergence and development for 1956 and 1957.

Larval emergence and development occur later in northern Wisconsin. In 1956, larval development was approximately three weeks later than in Madison in such northern areas as Iron County and Douglas County.

Host selection. Studies were conducted in September of 1956 and 1957 to test host tree preference for oviposition by adults reared from larvae on red pine. Equal size branches of red, jack, eastern white and Scotch pine (*P. sylvestris* L.) containing mature current and old needles were placed in water filler containers in screen cages in the red pine plantations at the University Arboretum. Adult males and females were released in the cages and the number of needles containing eggs were counted after oviposition was completed.

TABLE 2. Host selection by the red-pine sawfly.

Needles with eggs		Percent of total
Red pine	— 534	93.0
Scotch pine	— 27	4.7
Jack pine	— 13	2.3
White pine	— 0	0.0
Total	574	100.0

The sawfly exhibits a strong oviposition preference for red pine (Table 2). It laid eggs on Scotch pine (*Pinus sylvestris* L.) and jack pine, but all attempts to induce oviposition on eastern white pine were unsuccessful. Tests also were conducted with adults reared on jack pine. These adults showed a 100 percent preference for red pine; 123 needles of red pine contained eggs, but no oviposition occurred on other pines. In some areas of Canada, jack pine was preferred, while in others red pine was selected (Atwood *et al.*, 1943).

Host resistance. Egg mortality in needles of the host tree was observed during studies conducted to determine the percentage of larval emergence from overwintering eggs in the University Arboretum in 1956 and 1957. Each year the number of eggs in 20 colonies was counted and first instar larvae were collected daily as they emerged. The emergence from the overwintering eggs was 72 percent in 1956 and 77 percent in 1957. It was apparent that some needles were injured during oviposition, resulting

TABLE 1. Larval development in relation to temperature accumulation.

	Larval emergence			Larval development		
Year	Date	Day-degrees	Date completed	Days	Day-degrees	Total day-degrees
1956	May 14	308.5	June 12	29	672.7	981.2
1957	April 30	307.6	June 10	41	674.3	981.9
Mean		308.1		35	673.5	981.6

in needle mortality and subsequent egg mortality. The entire needle was not killed, but only the apical portion including the eggs. All or some of the eggs in these needles may be killed.

The percentage of larval emergence determined in this manner is subject to error, as some of the emerging larvae may have dropped from the twig, or may have been taken by predators. The actual percentage of emergence may be greater than the observations indicated.

An apparent resistance of jack pine to oviposition by the red-pine sawfly was observed in the University Arboretum. In these "resistant" jack pines, all needles with red-pine sawfly eggs died. These needles dropped in 3 to 4 weeks, although some remained on the tree over winter. Needles with eggs showed evidence of disturbance within 2 to 4 days after oviposition. The presence of one egg often caused a chlorosis of the needle tissue which spread outward from the egg pocket. The needle died soon after the chlorosis had spread across the width of the needle. This "resistance" was observed in two of 14 jack pines tested in the Arboretum. On other jack pines, the eggs remained alive over winter and larvae emerged in spring and completed their development.

Oviposition by red-pine sawfly adults was obtained on Scotch pine at the Griffith State Nursery at Wisconsin Rapids. Egg laying by 13 mated females did not injure the needles, which remained healthy throughout the winter. The 13 colonies were checked on June 1, 1957, at which time third and fourth instar larvae were present on nearby red pines. No evidence of larval feeding was observed in four of the 13 colonies on the Scotch pine. The other nine colonies all had evidence of first instar larval feeding, and cast skins of the first instars were present. There was no feeding beyond the second instar. The possibility that a predator destroyed the larvae cannot be discounted, but it is unlikely that all 13 colonies of larvae were destroyed. Scotch pine is thus suspected of being repellent or perhaps toxic to young red-pine sawfly larvae.

Similar occurrences have been reported with other sawflies and host trees. Benjamin *et al.* (1955) reported resistance of pitch pine, *P. rigida* Mill., to oviposition by the European pine sawfly, *N. sertifer* (Geoff.), in the Henderson State Forest in Illinois. Following oviposition by *N. sertifer*, pitch pine needles died and dropped. Tsao and Hodson (1956) conducted studies on the effect of different host species on the oviposition and survival of the introduced pine sawfly, *Diprion similis* (Htg.) This sawfly preferred white pine for oviposition, and considerable larval mortality occurred on mugho pine.

Natural Control

The influence of natural control factors on the red-pine sawfly in Wisconsin has not been studied previously. Data are available only from Ontario, where Schedl (1938) investigated the biotic and abiotic factors, and Coppel (1954) and Raizenne (1957) listed the insect parasites.

Infestations of the sawfly at the University Arboretum, and particularly at the Poynette Game Farm where numbers were high, provided an opportunity to study the effects of natural control on this pest.

Abiotic factors. The red-pine sawfly is quiescent approximately ten months of the year and at a time when weather conditions are most severe. Little is known of the effects of physical factors during this period. However, eggs in the needles of the host tree are apparently not adversely affected by common low temperatures as evidenced by their survival in northern Wisconsin where temperatures often drop to −40° F.

Red-pine sawfly larvae emerge and develop in spring during a period of usually moderate temperatures. Temperature extremes during the larval feeding period in 1956 were 34° F and 96° F and in 1957 30° F and 88° F. The larvae seek protection among the bases of the needles during rainstorms and resume feeding after the storm ceases.

The summer is spent in cocoons in the forest litter, where they are protected from extreme temperatures. Heavy rains do not affect these cocoons, as they are relatively impermeable to water. Adults emerged from a small number of cocoons experimentally floated in water for two weeks during the summer.

Adults emerge in the fall, mostly during September, when temperatures are moderate. The adults are inactive on cold days but resume mating and oviposition activities as soon as the temperature rises. Oviposition has been observed at 45° F and higher temperatures.

Parasites. Schedl (1938) reported two percent destruction of red-pine sawfly eggs by unidentified parasites in Ontario. Egg parasites were not observed in the current study.

Data on parasites reared from the larva and cocoon collections from Poynette are presented in Table 3. The only parasites reared from the Arboretum larval collections were *P. hamata* (A. & W.) and *E. canadensis* Prov. One hyperparasite, *Eupelmella vesicularis* (Retz.), was reared from the introduced cocoon parasite, *D. fuscipennis* (Zett.).

The most important parasite of the sawfly was the introduced cocoon parasite, *Dahlbominus fuscipennis* (Zett.). When it became established in the Poynette area has not been determined. The nearest point of release was at Arkdale, Wisconsin, in 1955, about 50 miles northwest of Poynette. *D. fuscipennis* is particularly effective against the red-pine sawfly because the cocooned sawflies are present throughout the summer. The cocoons are present in the forest litter rather than in the mineral soil, thus permitting them to be located readily by this efficient parasite.

The cocooned larvae are attacked throughout the summer by successive generations until adult sawflies emerge in fall. *D. fuscipennis* is able to complete its development even after pupation of the sawfly has occurred. Few cocoons are parasitized in early summer, but the population builds up rapidly later. The number of cocoons destroyed has been omitted in Table 3, as the cocoons were collected in early summer when only a few of these parasites emerged.

D. fuscipennis emergence holes can be recognized easily; they are about 0.8 mm in diameter. The number of cocoons destroyed by this parasite, determined from fall collections, is shown in Table 4.

The greatest degree of parasitism by the Ichneumonidae occurred after the lavae dropped from the trees and were crawling over the litter searching for a cocooning site. Large numbers of *E. subclavatus*, *E. canadensis*, and *M. argeae* were swarming over the litter at the Poynette plantation at the time the larvae were dropping from the trees in early June. *P. hamata* and a few *E. canadensis* were reared from larvae collected on trees, but cocoons collected shortly after they were spun yielded many more.

Predators. No predators were observed feeding on eggs of the red-pine sawfly. A pentatomid bug, *Euschistus variolarius* (P.

TABLE 3. Parasites of the red-pine sawfly Poynette, Wisconsin[1]

	Number
HYMENOPTERA	
Eulophidae	
Dahlbominus fuscipennis (Zett.)	[2]
Ichneumonidae	
Endasys subclavatus (Say)	277
Exenterus canadensis Prov.	83
Mastrus argeae (Vier.)	64
Agrothereutes sp.	4
Delomerista sp. *diprionis* group	2
Euceros sp. nr. *thoracicus* Cress	1
Lamachus sp.	1
Eupelmidae	
Eupelmella vesicularis (Retz.)[3]	2
DIPTERA	
Larvaevoridae	
Phorocera hamata (A. & W.)	7

[1]Determinations of the sawfly parasites were made by the U. S. Dept. Agric. Insect Identification and Parasite Introduction Laboratories, Beltsville, Maryland.

[2]See Table 4.

[3]Hyperparasite of *D. fuscipennis*.

TABLE 4. Percentage of parasitism by D. fuscipennis.

Year	Total parasitized cocooned larvae	Number parasitized by *D. fuscipennis*	Percentage of *D. fuscipennis*
1955	1480	962	65.0
1956	1105	431	39.0
1957	263	195	74.2

TABLE 5. Control factors associated with cocooned red-pine sawflies.

	1955		1956		1957	
	Number	Percent	Number	Percent	Number	Percent
Adults	231	8.15	517	13.08	53	1.38
Small mammals	590	20.82	1858	47.00	2996	78.12
Parasites	1480	52.22	1105	27.96	263	6.86
Fungus	229	8.08	310	7.84	484	12.62
Unidentified	304	10.73	157	3.97	37	0.97
Diapause	0	0.00	6	0.15	2	0.05
Total	2834	100.0	3953	100.00	3835	100.00

de B.), was collected feeding on a fifth instar larva.

Lynx spiders, *Oxyopes salticus* Hentz, were observed preying on all five instars of the sawfly (Fig. 9), at the University Arboretum and Poynette plantations. They often can be found sunning themselves on the developing shoots of red pine, particularly on warm spring days. The control exerted by this species is difficult to evaluate, but at the University Arboretum several entire colonies were destroyed. In heavy infestations, *O. salticus* probably exerts only a minor influence on the total population, but they may be important control factors in light infestations.

Birds have not been reported feeding on red-pine sawfly larvae in Wisconsin, although Schedl (1938) stated that song birds fed readily on larvae in Ontario. He reported 70.8 percent of the original population destroyed by birds, predatory wasps and ants.

Small mammals are the most effective cocoon predators at the Poynette infestation. Mammalian predation began as soon as the larvae dropped to spin cocoons in the litter and continued until adult emergence in the fall. The percentage of cocoons destroyed by small mammals in the Poynette plantation is listed in Table 5.

Treadle traps and snap traps were used to collect small mammals in the plantation.

FIGURE 9. *Lynx spider,* Oxyopes salticus, *attacking fourth instar larva.*

Peanut butter and small bits of bacon proved the most effective bait, although the mammals did take cocoons readily. The only species of mouse collected was the white-footed woods mouse, *Peromyscus leucopus* (Rafinesque), (Fig. 10).

Caged white-footed woods mice devoured up to 100 cocoons in a 24-hour period. They preferred sawfly cocoons, even when an ample supply of other food was available. Mice raised in captivity opened the cocoons and ate the prepupal larvae as readily as did mice collected in the plantation. They usually rejected the head capsule and all or part of the thorax if an ample supply of cocoons was available; however, they ate the entire prepupa if only a few cocoons were offered. Head capsules were not found among the stomach contents of mice trapped in the plantation.

Feeding mice under cage conditions obviously does not establish that they consume equal numbers of cocoons in a 24-hour period in the plantation. However, examination of stomach contents and the strong preference for sawfly cocoons indicates that the destruction of 100 cocoons overnight is possible if the cocoons are plentiful. The mice at the Poynette plantation at first fed upon the cocoons that could be found easily on the surface, then burrowed into the litter as the supply dwindled.

FIGURE 10. *White-footed woods mouse*, Peromyscus leucopus, *feeding on cocooned sawfly larvae.*

The white-footed woods mouse does not differentiate between sound, parsitized, or diseased cocoons, but cocoons with fungus killed prepupae are often bitten into and then rejected. The actual control by mice is difficult to assess because of the interference with parasites. The mice also devour larvae as they crawl about on the forest litter before spinning cocoons; no attempt has been made to estimate the numbers destroyed.

Cocoons emptied by mice can be distinguished readily from those from which adult sawflies or parasites emerged (Fig. 11). Those opened by mice often bear incisor teeth marks, and in general, the openings are ragged compared to adult emergence holes. Mice empty the cocoons by biting off the end and pulling out the larvae, although a small number open the cocoons on the side. This is an individual characteristic, and mice that opened cocoons on the side did so consistently; mice opening cocoons on the end were also consistent. Slightly more than one percent of the cocoons opened by small mammals

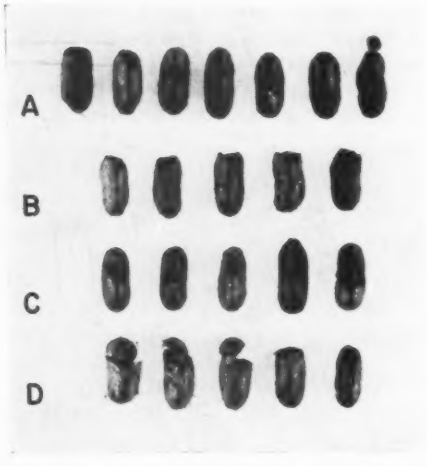

FIGURE 11. *Red-pine sawfly cocoons illustrating variety of exit holes and predation damage. A. Left to right: adult sawfly, woods mouse (end), woods mouse (side),* D. fuscipennis, E. subclavatus, E. canadensis, P. hamata. *B. Cocoons opened on end by woods mouse. C. Cocoons opened on side by woods mouse. D. Cocoons opened on end by eastern chipmunk.*

were opened on the side in 1955 and 1956, and six percent in 1957.

The eastern chipmunk, *Tamias striatus* (Linnaeus), also fed on cocoons at the Poynette plantation. Cocoons opened by these mammals are difficult to separate from those opened by mice (Fig. 11). Chipmunks remove a slightly larger bite from the end of the cocoon. Examination of the stomachs of chipmunks yielded little information because of the well-masticated condition of the contents. Relatively few chipmunks are present in the plantation, and it is believed that the number of cocoons destroyed by them at the Poynette plantation is small. Schedl (1938) reported the feeding of eastern chipmunk on cocoons in Ontario, but gave no quantitative information on the amount of predation.

Shrews were not trapped or observed at Poynette plantation, nor were any cocoons identified as opened by them. However, they are reported to be important mammalian predators of sawfly cocoons by Buckner (1955), Holling (1955) and Morris (1949). It is generally considered that these insectivorous forms possess a greater ability to distinguish sound from diseased or parasitized cocoons. This, coupled with their higher food requirement would make them effective predators.

Little is known of predators attacking adult sawflies; the only predator collected was a pentatomid bug, *Euschistus politus* Uhler. Undoubtedly, some bird predation occurs, but this is thought to be insignificant.

Diseases. A number of the cocooned larvae were destroyed by a fungus identified as a strain of *Beauveria bassiana* (Bals.) Vuill.[2] at Poynette. The percentage destroyed during 1955 to 1957 is shown in Table 5.

Evaluation of mortality of cocooned sawflies. Larvae of the red-pine sawfly spend 3 to 4 months in cocoons in the forest litter. During this period they are subject to intense predation by small mammals and parasitization by ichneumonid wasps. Cocoon samples were collected at the Poynette plantation from 1955 to 1957. In 1956 and 1957, collections were made at the time of adult emergence in the fall, after they had been exposed to all the natural control factors during the summer. The 1955 cocoons were collected in the summer of 1956, before the 1956 cocoons were formed. The cocoons were examined singly and the fate of each was determined. Small mammals, parasites and fungus are the most important biological control agents of the cocoon stage (Table 5). In most cases, the cocooned larvae classified as unidentified died before pupation. A higher percentage of cocoons appears in the unidentified column for 1955 because these collections were made in the summer of 1956. Some deterioration had occurred, making it more difficult to determine the cause.

The percentage of sawflies destroyed by fungus did not vary as greatly in the three-year period as that destroyed by small mamals and parasites. Destruction of cocoons by small mammals was caused by the white-footed woods mouse, *P. leucopus*. The mice apparently devour parasites as readily as sawflies. The increase in the mouse predation over the three-year period is reflected in a decrease in the number of cocooned larvae destroyed by parasites.

Defoliation Injury to Host Tree

The red-pine sawfly completes larval feeding in early June in southern Wisconsin. The new needles have not fully developed, being only about 1 to 1½ inches long at this time. They are not fed upon by the larvae, which feed only on the old needles put on during previous seasons. Red pine normally retains old needles for 3 to 5 years (Fig. 12). If there is a heavy infestation, all the old foliage will be consumed, leaving the new needles and the stubs of old needles (Fig. 8, 13). The tree regains one year's foliage after the new growth is completed. This enables the trees to recover

[2]Identification of the fungus was made by the Insect Pathology Laboratory of the Canada Department of Agriculture Science Service, Sault Ste. Marie, Ontario.

FIGURE 12. *Normal foliage of red pine.*

from the effects of defoliation (Fig. 14).

Measurements of the annual height growth of defoliated and non-defoliated trees at the Poynette plantation were taken on trees of similar size. The trees were about 30 to 35 feet in height, and 17 trees were measured in each group. The infested trees were severely defoliated in 1955 and 1956, and light defoliation (10 percent) occurred in 1957. An estimated 5 percent defoliation occurred in 1957 in the trees not previously defoliated. Whether this had an effect on the 1957 growth is difficult to ascertain. Measurements were taken back to 1944, to enable comparison of the two groups of trees.

The first heavy defoliation at the Poynette plantation occurred in 1955, and was reflected in an average 21 percent height growth reduction (Fig. 15). Part of this reduction may be the result of partial defoliation in years prior to 1955. In 1956, only one year's growth of needles, instead of the usual three, was present on these trees. These old needles were quickly consumed and growth was reduced 64 percent.

Defoliation in 1957 was about 10 percent in the previously heavily defoliated trees, yet the growth rate was 70 percent less than that of normal trees. This undoubtedly resulted from the previous two years of heavy defoliation. In the spring of 1957, only one year's foliage was present, and these needles were smaller and fewer in number than on non-defoliated trees.

No mortality of red pine occurred at the Poynette infestation. Red and jack pines are very susceptible to sawfly injury and one complete defoliation by *N. lecontei* will kill them. (Benjamin, 1955). Defoliation by the red-pine sawfly does not affect red pine as severely because the destruction of old needles only allows the tree to regain a year's foliage as soon as the new growth is completed. The one-inch stubs remaining from defoliation may possibly assist in tree survival, as they remain green until mid-summer. The exact value, however,

FIGURE 13. *Severely defoliated red pine. Poynette, Wisconsin. June 16, 1957.*

FIGURE 14. *Same trees as in Figure 13 after new shoot growth, August 20, 1957.*

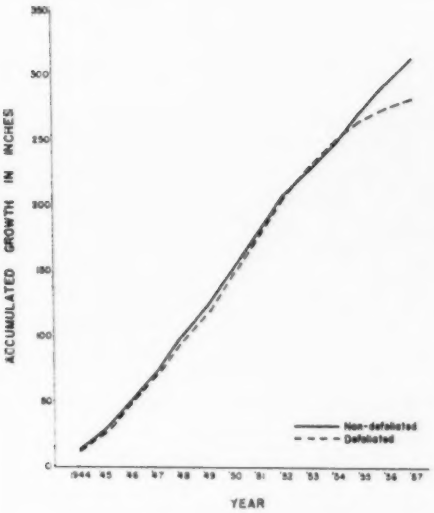

FIGURE 15. *Comparison of height growth of defoliated and nondefoliated red pine.*

has not been determined.

From observations of the infestation at the Poynette plantation, the following conclusions are drawn:

1. Defoliation by the red-pine sawfly does not affect red pine as severely as defoliation by the red-headed pine sawfly, *N. lecontei.*

2. One complete defoliation of red pine by the red-pine sawfly is reflected in a 21 percent reduction in height growth.

3. Two successive years of defoliation will reduce height growth as much as 64 percent, but will not cause mortality if the trees are vigorous.

The good vigor of the red pine at Poynette must be considered an important factor in enabling the trees to withstand sawfly attack. Red pine in poor condition undoubtedly would have been affected more seriously.

Summary

Biological and ecological studies of the red-pine sawfly, *Neodiprion nanulus nanulus* Schedl, were conducted in 1955, 1956 and 1957 at the Poynette Game Farm in Columbia County, and at the University Arboretum in Dane County, Wisconsin.

One generation of the sawfly occurs annually, with only a small number of larvae remaining in diapause. The sawfly overwinters in the egg stage in the new needles of the host tree. Larval emergence occurs in early May in southern Wisconsin. Five feeding instars are completed by female larvae and four by males in 4 to 6 weeks. The cocoons are spun in the forest litter in June, and adults emerge in the fall. Oviposition occurs shortly after emergence.

An average 58.2 percent females emerged from larvae collected and reared in a 3-year period. The number of eggs per female was 51.6 ± 8.3. An average of slightly more than two eggs per female remains after oviposition. The eggs are placed in a series of pockets cut in pine needles. From 4 to 13 eggs per needle in red pine were most commonly found, and 9 eggs per needle occurred most frequently. The females usually deposit the entire egg complement on one twig.

The larvae feed gregariously on old needles of the host tree. The first two instars eat only the outer layers of the needles. The third, fourth and fifth instars devour the entire needle, and leave a characteristic one-inch stub on red pine. One complete defoliation by the red-pine sawfly will not seriously affect red pine. Heavy defoliation for two successive years will reduce height growth by 64 per cent. No mortality was observed after two years' defoliation.

Phenological observations and temperature accumulation data in relation to larval emergence and feeding are presented. Some degree of resistance by jack pine was observed in the University Arboretum. This was manifested in needle drying shortly after oviposition, with subsequent egg mortality.

Natural control factors exert heavy pressure on this sawfly. Some egg mortality results from red pine needle drying. Nine species of parasites have been reared. The

most important of these is the introduced parasite, *Dahlbominus fuscipennis* (Zett.). Heavy predation of cocooned larvae occurs during the summer, principally by the white-footed woods mouse, *Peromycus leucopus* (Rafinesque). A fungus, *Beauveria bassiana* (Bals.) Vuill., also destroys a number of larvae. The cocooned stage is the most vulnerable; in 1957, 97.6 percent of the cocoons sampled were destroyed by parasites, predators and fungus.

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The Forest Ranger

By Herbert Kaufman. 259 pp. Johns Hopkins Press, Baltimore, for Resources for the Future, Inc. 1960. $5.

Review by Myron Krueger, Professor of Forestry, Emeritus
University of California

It should be pointed out at the outset of this review that the title of this book, without the inclusion of the subtitle, "a study in administrative behavior," can be quite misleading to the prospective reader. Perhaps the subtitle should have been the main title, with an accompanying subtitle "as evidenced by the United States Forest Service." This would have been more expressive of the contents of the book. However the reader is duly warned as to the object and contents, both in the foreword by Marion Clawson of Resources for the Future, Inc. and in an excellent preface by the author.

The author, an Associate Professor of Political Science at Yale University, is apparently impressed by the outstanding success of the U. S. Forest Service in securing compliance with the policies established at the top of the administrative ladder by the ultimate field representative, the Forest Ranger. The author, as a researcher in political science, very wisely and properly avoids any discussion of whether these policies are good or bad and confines himself to the reasons for maintenance of these policies by the most remote (in the administrative hierarchy) representative.

For his study, the author has confined himself to five ranger districts. In the opinion of this reviewer, the districts were well chosen. His later discussion of the problems involved and their solution by the Forest Service should satisfy any informed reader that the author has gathered data, entirely sufficient for the thesis which he presents.

It is the viewpoint of the author that in a land management problem such as confronts the Forest Service, the Forest Ranger of necessity becomes pivotal in seeing to it that the land management objectives of the Service are carried out. By the very nature of the diversity of objectives among the many ranger districts, due to wide differences in the land resources and in the pressures of the surrounding population, one should expect a centrifugal tendency toward highly autonomous action by each ranger. These tendencies are discussed in detail in Chapters II and III. Then follow three chapters on the basic reasons (from the standpoint of political science) for the predominance of integrating influences over the centrifugal tendencies. The most prominent integrating influences are the preformed decisions at the higher levels of administration, the *Forest Service Manual*, a multiplicity of reports from and directives to the lower echelons, the preparation of resource and other plans (in which the Ranger has participated to some degree), frequent inspections, and the transfer of personnel. It is the personnel policy of the Service to discourage deviation, but this policy is made more acceptable through the development of a genuine "esprit de corp."

To one who completed his professional forestry education prior to 1920 and has thus has had the opportunity for 40 or more years of observing the activities of the Forest Service, the book is particularly interesting in pinpointing the main factors for the successful performance of the Service and in explaining why this organization has been free of the scandals associated with the land custodianship of some of the governmental agencies which preceded the Forest Service. The discourse is all the stronger for being a study in administrative behavior rather than a sentimental treatise.

In looking ahead to the time when the objective of the Forest Service must be much more largely that of making the land produce up to its full capacity of the resources needed (not necessarily desired) by a greatly increased population rather than objectives quite largely of administrative procedures, will the Forest Service be able to employ the same devices for securing compliance in the field? The author apparently has some misgivings along this line in his concluding chapter. But the reader is left with the impression, subtly suggested by the author, that the future leaders of the Forest Service will prove as capable of finding devices to secure Service-wide compliance with objectives applying at their time as have the leaders of the past and present.

Some Evidences of Premature Stoppage of Sugar Maple Sap Production

BY
TE MAY CHING
LEO W. MERICLE

MAPLE SAP PRODUCTION during a season is often limited by the premature stoppage of sap flow. Quite often the dried tap holes show definite microbial infection. Recently, Naghski (1953) and Naghski and Willits (1955) concluded that this premature stoppage was attributable to the invasion of bacteria and possibly other microorganisms. Their conclusions, were based upon bacterial counts, no histological observations of the maple tissue being made. Since a true microbial invasion can usually be detected from histological slides and since an actual physical plugging should be reflected in histological materials if proper care is given, a thorough investigation of the tissue around normally tapped holes was carried out at selected intervals during the sap season of 1955. At this time there seemed to be no apparent change at the tissue level when the sap was free-flowing, yet signs of microbial invasion were clearly indicated from studies of the tissues around dried tap holes at the end of the sap season.

To further elucidate the mechanism of premature stoppage, an experiment was performed in 1956 to compare sap production and the degree of microbial infection following three kinds of tapping: (1) normal non-sterile tapping, (2) sterile tapping, and (3) sterile tapping followed by deliberate inoculation with known microorganisms.

This present paper reports the histological findings and some preliminary observations concerning the mechanism of stoppage of sugar maple sap production. Other results of this study, regarding bacterial counts, isolates, and sap production, will be published separately.

Materials and Methods

Histological study. Thirty sugar maple trees of 20-inch diameter or greater, located in the experimental woodlot of Michigan State University, were tapped in February, 1956. Each tree was triply tapped by the three types of tapping mentioned above. Sap production from each tap hole was recorded daily and bacterial counts of the sap were checked at definite intervals (this part of the work was done by the Departments of Forestry and Microbiology). Toward the middle of the sap season, 12 of the 30 experimental trees already showed a high degree of contamination within the inoculated

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This paper reports, in part, work supported by U. S. Dept. of Agriculture Contract No. A-1s-33847 in cooperation with the Departments of Forestry and Microbiology, Michigan State University. Manuscript received May 11, 1959.

tap holes, some being completely dried.

Materials for histological study were taken from trees of this contaminated group by keeping the two following criteria in mind: (1) only trees which produced approximately the same total amount of sap from all three tap holes normally expected from an equal sized tree were selected, and (2) only trees which showed a differential production of sap among the three specific tap holes were selected (sterile tap holes produced the highest total amount of sap, while inoculated ones yielded the least). Tissue around each tap hole was collected, half being fixed in FAA (15 parts formalin, 15 parts glacial acetic acid, 70 parts 70 percent ethanol, by volume), and the other half either sectioned as fresh material or kept frozen for later use. An additional group of samples having the same history was collected at the end of the sap season.

In order to study the actual condition of fresh materials from the three kinds of tapping, sections (approximately 40 μ thick) were cut with a freezing microtome modified for this purpose, stained with 0.1 percent neutral red and immediately examined for the relative infestation of microorganisms. Additional duplicate materials were killed and fixed, embedded in paraffin by standard histological procedures and cut into thinner sections (16-18 microns) with a Spencer sliding microtome. These sections were then stained either with Pianese IIIB or a modification of Conant's quadruple stain (Johansen, 1940), and prepared as permanent slides for detailed histological study.

Physiological study. Three bacterial cultures (*Pseudomonas* spp.) which had been isolated in 1955 from normally tapped holes, and used for the deliberate inoculation of trees in 1956 were inoculated into 50 ml of 0.3 percent beef-extract containing 0.1 percent pectin and incubated on a shaker for 72 hours at 25°C. Cells were then harvested from the liquid culture by centrifugation (10 minutes at 24,000 × g). After re-suspending the resulting bacterial pellets in 5 ml sterile glass-distilled water the suspension was tested for the formation of gummy substances and for the determination of pectolytic activity.

Sterilely collected and normally collected samples of sap were processed in the following manner: sterile sap was concentrated by alternate freezing and partial thawing to approximately 0.01 of its original volume, i.e., 2000 ml of sap was concentrated to a 20 ml volume, while normal sap was lyophilized and re-suspended in sterile water to a final concentration of 5×.

Results

Normal non-sterile tapping. From the fresh, frozen sections marked infestation by yeasts, molds, and bacteria was clearly evident. Thick crusts of microflora lined the dried tap holes. These crusts were composed of a network of mycelium (both septate and non-septate branching hyphae) with scattered yeast cells and gummy deposits containing tremendous numbers of bacteria (bacilli, 2-4 μ in length, 0.2-0.5 μ in diameter; cocci, 0.5 μ in diameter) (Fig. 1). Only remnants of the microflora, however, could be found in the permanent histological preparations. As a result of the numerous washings and dehydrations during the standard paraffin embedding and staining,

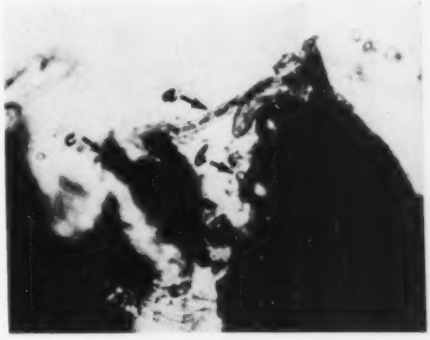

FIGURE 1. *Fresh longitudinal section of normally tapped maple tissue showing septate hypha (a), yeast cells (b), and bacteria embedded in dark gummy substances (c).*

only a small percentage of the original population was still present.

Within the tissues around the tap hole, yeast cells were sporadically found in vessel elements and living cells adjacent to the larger vessels. Their numbers became enormous toward the end of the season. Bacteria were "embedded" in gummy substances which partially or wholly filled the vessel lumens and chambers of bordered and half-bordered pits of the vessel walls (Fig. 2). Bacteria were also observed scattered through all types of cells and at times penetrating to a depth of 5 mm above or below the tap hole, but more limited in their horizontal spread. Fungal hyphae were occasionally seen in vessels and other types of cells (Fig. 3).

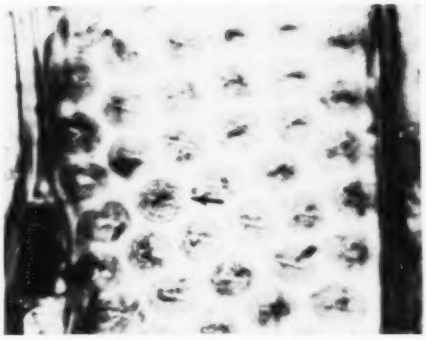

FIGURE 2. *Permanent longitudinal section of vessel wall showing bacteria-infested chambers and cannals of bordered pits.*

Sterile tapping. From the frozen sections no sign of microorganisms could be detected. Only the dried sap, oxidized cellular contents, and tapping debris lined the tap holes. The same situation was true in the permanent (paraffin embedded) slides.

FIGURE 3. *Permanent tangentional section of tissue 2 mm. from tap-hole showing infested fungal hypha (a), and bacteria embedded in gummy substances (b) in vessel.*

Inoculated tapping. Bacterial invasion was well demonstrated within tissue surrounding the tap holes of this material. The organisms were congested in vessel elements and had invaded the neighboring parenchymatous tissues as well as the wood fibers (Fig 4). The torus and primary wall between adjoining bordered pits were dissolved and gummy substances were formed in pit channels and pit chambers (Fig. 5). Infested areas at times extended 6-7 mm below the tap holes, but to a lesser extent above them.

The Mechanism of Premature Stoppage

Vessel blockage. The open lumens of vessel elements surrounding the inoculated and normal non-sterile tap holes were prevailingly plugged with gummy substances, brownish in color and containing numerous bacteria. These substances are evidently produced by the invading organisms alone or from an interaction between the organisms and the maple tissue and sap. An attempt was made, therefore, to determine the relationship, if any, between the formation of the gummy residue and maple sap.

For this purpose, 2.5 ml of concentrated maple sap (collected by sterile tapping) was incubated at 30°C for 24 hours with 5 ml of the previously isolated bacterial suspension. Results in Table 1 show that vitality of the bacterial suspension is not essential but that non-boiled sap is necessary, for the formation of a gummy residue. This gummy residue was found to have the same staining properties and apparent physical consistency as the gummy plugs within vessel elements of the maple tissue. It thus seems probable that the gummy material composing the plug is induced by the bacteria and a normal constituent of the maple sap.

When concentrated normal (non-sterile) sap, containing yeast cells as well as bacteria, was tested in a similar manner for the formation of gummy substances, a larger quantity of residue was obtained.

TABLE 1. Results of incubation of bacterial suspensions and sterilely collected, concentrated maple sap.

Bacterial suspension	Maple sap		
	None	Boiled	Unboiled
None	...	Precipitate	Albuminous
Boiled	Milky	Precipitate	Gummy residue
Unboiled	Milky	Precipitate	Gummy residue

Bacterial penetration into living cells. The observation that bacteria occurred on both sides of the bordered pits and half-bordered pits indicates a true invasion of plant tissue by the microorganisms. This has also been shown to be the case in verticillium wilt and bacterial wilt in plants, wherein the microorganisms dissolve cell walls by the action of pectinases (Kelman 1953, Scheffer *et al.* 1956). Therefore, an attempt was made

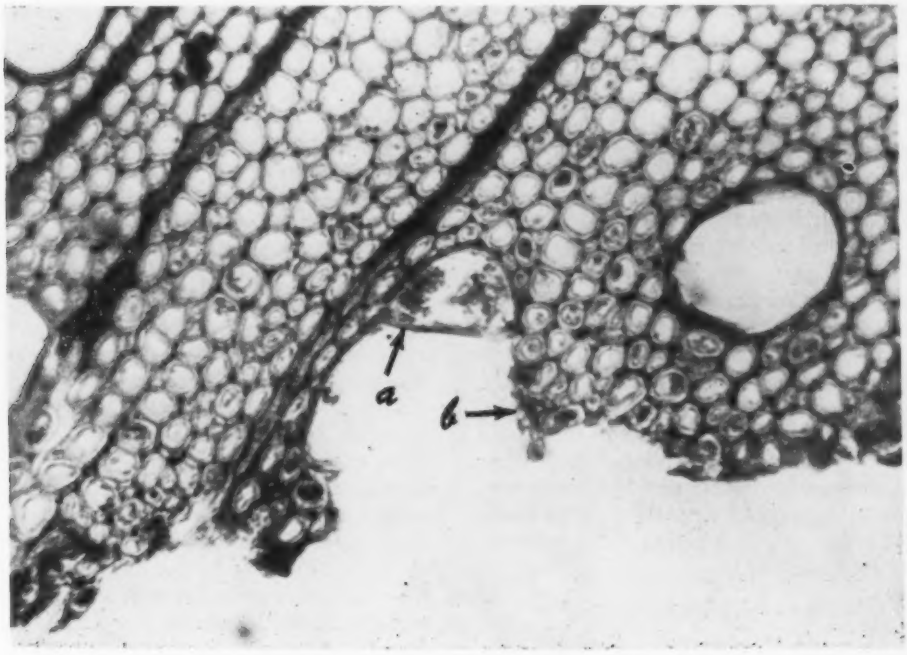

FIGURE 4. *Permanent cross section of tissue around innoculated tap-hole showing the abundance of yeast cells (a) and bacteria embedded in gummy substances (b) in vessels, fibers and ray cells.*

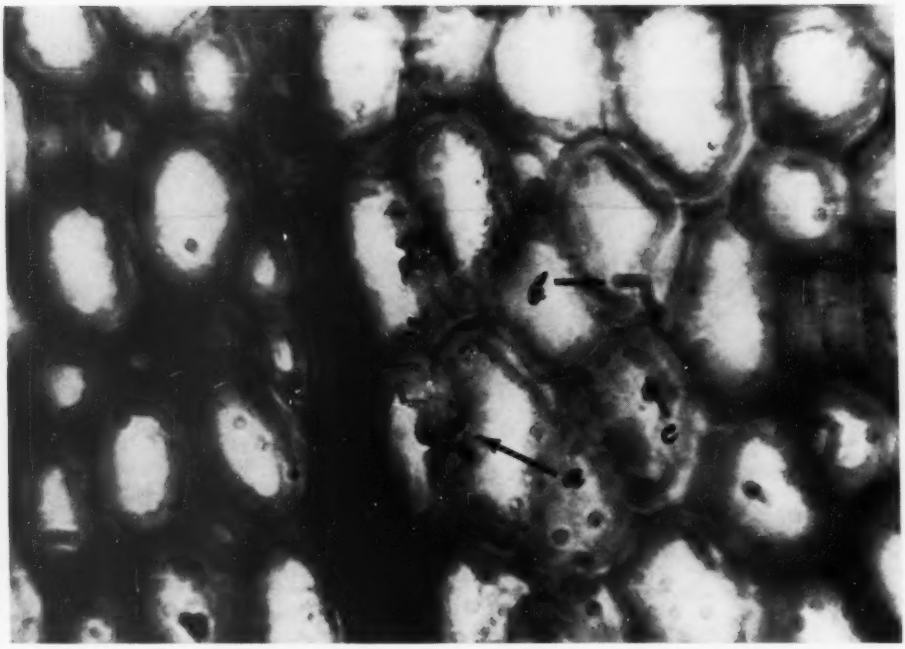

FIGURE 5. *Permanent cross section of infested tissue showing irregular cell lumens of fibers, dissolved cell wall with gummy plug (a) fungal hypha (b), bacteria (c), and gummy substances in ray cells.*

to demonstrate pectolytic activity of the isolated bacteria by utilizing a standard method (Bell *et al.* 1950) of measuring the viscosity changes in a pectin solution. An average of ten percent reduction in viscosity was observed in a non-boiled as compared with a boiled suspension after 45 minutes incubation at 30°C. Conceivably, even greater reduction might have been obtained by increasing the incubation time and increasing the pH as has been pointed out by Kelman (1953) and Kertesz (1951). It seems reasonable, therefore, that these microorganisms possess pectolytic activity and that this activity may provide a mechanism by means of which pathogenic penetration is accomplished.

Discussion and Conclusions

Observations that bacteria can induce the formation of gummy substances in vitro and that these apparently are the same gummy substances which make up the plugs within vessel elements which surround normal and inoculated tap holes indicates the possibility of an actual physical plugging of the sap ascending pathways. Similar gummy plugs containing bacteria have been observed in various species of plants infected by bacterial wilt, *Pseudomonas solanacearum*, whereby plugging hinders water transport in the plant, then wilting occurs (Kelman 1953). The same mechanism may hold true in the case of sugar maple.

In addition to the physical plugging, a physiological disturbance may also be indicated by the fact that bacteria were present in all types of cells adjacent to the vessel elements. These bacteria apparently enter the open lumens of cells surrounding the tap hole, thence invade the living cells via adjacent pits conceivably as a result of their pectinase activity. In spite of the different opinions regarding the mechanisms of sap

flow (Johnson 1945, Marvin and Erickson 1956, Marvin and Greene 1951, Stevens and Eggert 1945, Wiegand 1906), many workers in the field consider living cells to be the vital controlling centers. Since bacteria can readily invade living cells of the maple tissue, it is reasonable, therefore, to believe that the physiological functions of such cells might become so altered that normal sap flow would be affected.

Microorganisms other than bacteria are probably not directly responsible for *premature* stoppage. The appearance of yeast cells is limited to only the warmer weather toward the end of the sap season and their penetration into the tissues apparently follows bacterial invasion. The scarcity and inconsistent localization of fungal materials limits their significance in premature stoppage, although they may exert a secondary effect near the end and/or after the sap season, causing infection and discoloration of the tissues.

Summary

Histological findings indicate that premature stoppage of sap flow in normally tapped maple trees results from the combined effects of a bacterial invasion of the living tissue via pits along the cell walls, and an actual vessel blockage by microorganisms and/or gummy plugs produced by these microorganisms. Demonstration of pectolytic activity in the bacteria isolated from tap holes suggests a mechanism whereby these organisms penetrate the pit membranes.

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A New Method of Growth Ring Analysis And the Determination of Density by Surface Texture Measurements

BY
J. E. MARIAN
D. A. STUMBO

WHILE STUDYING the influence of anatomic structure on adhesion in wood (Marian *et al.*, 1958), it was observed that a tracer instrument[1] could determine details of anatomic structure, such as cell-cavity or cell-wall dimensions, and distribution of springwood and summerwood within the year's growth ring (Fig. 1). This suggested that if quantitative data could be obtained the result would be a new approach to growth ring analysis and determination of density. The method would be free from human errors inherent in existing methods, would be more accurate, and would even permit the recording of detail within the springwood-summerwood sections rather than in only the border lines between them. This report is based on such an approach. The basic considerations concerning measurement of the surface texture of wood have been treated elsewhere[2] and are not considered here.

Existing methods of growth ring assessment are based essentially on linear microscopic measurements of growth ring widths by individual observers (Eklund, 1949; Jazewitch *et al.*, 1957) and the accumulation of measurements by mechanical (Eklund) or electrical (Huber) means. Other methods, probably of historical interest only, are the photoelectric evaluation of microscopic cross sections developed by Müller-Stoll (1949), the hardness tester by Mayer-Wegelin (1950), and the H_2SO_4 etching method by Kisser and Lehnert (1951). The respective merits or deficiencies of these methods can be studied in the original references.

The instrument most widely used for large-scale investigations was developed by Eklund (1949) at the Swedish Forest Research Institute. Another instrument, recording electrically, was developed under the direction of Huber and Jazewitch at the Institute of Forest Botany at Munich (Jazewitch 1957). This uses fixed samples and the microscope moves on tracks (Trendelenburg and Mayer-Wegelin, 1955). An instrument for individual preparation and observation was devised by Keylwerth (1954).

[1]Talysurf and Talymin, by Taylor and Hobson, Leicester, England.

[2]Marian, J. E. Surface Texture in Wood—Theory, Methods, Applications. Forest Products Laboratory, University of California. (Manuscript in preparation.)

The authors are with the University of California's Forest Products Laboratory, Richmond. They gratefully acknowledge the inspiration received from the work carried out in F. Kollmann's institute in Munich, and from W. Ehler's monograph which was made available to them before publication in Holz a. R. u. W. and which materially aided the planning of this work. Manuscript received Aug. 14, 1959.

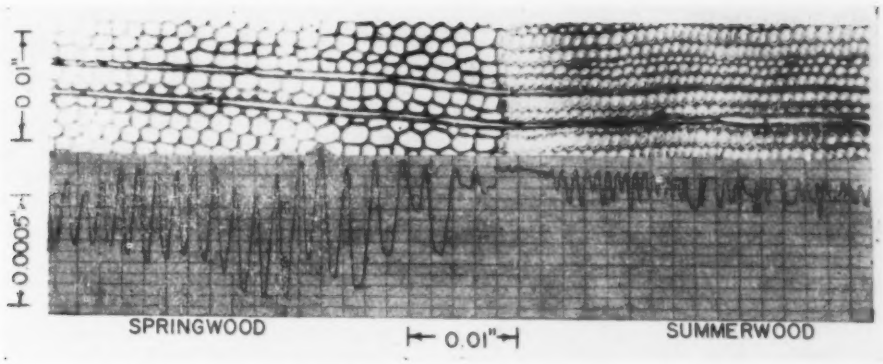

FIGURE 1. *Photomicrographs of Douglas-fir springwood and summerwood transverse surfaces with texture graphs at the same magnification.*

Ehlers (1958) attempted to determine the dimensions of anatomic details from surface texture measurements with a Leitz-Forster tracer type instrument but the sensitivity and resolution of the instrument, using a stylus with a 60μ tip radius, were inadequate. Morschauser (1954) used planimetric measurements of enlarged micrographs, and Liese and Meyer-Unlenried (1957) employed the Leitz "integration-stage" and "linear taxation" for the assessment of the relative amounts of the various anatomic constituents of woods. A comprehensive survey of growth ring research in different parts of the world was published in the Tree-ring Bulletin in 1956.[3] Research other than in dendro-chronology is, at present, not very lively in the United States. In Europe, however, techniques of growth ring analysis have increasing significance in forest botany, forest economies, forest genetics, and in studies of environmental growth factors of forest trees. All Scandinavian forests are measured by the so-called "linear taxation" method based on increment cores—the system developed mainly by Eklund (1949). Because of the various possible applications of growth ring analysis it would seem that a more detailed, rapid, and accurate method of conducting such research would have great utility.

[3]Published by the University of Arizona.

Growth Ring Analysis by Surface Texture Measurements

Essentially, the new method proposed here consists of transformation of mechanical movements of a stylus into electrical current impulses which are recorded instantaneously as graphs of the magnified surface, or are averaged in terms of some conventional value such as center line average (C.L.A.), root mean square (R.M.S.), or "crest line average" measures. These electrical impulses could also be preserved as coded data, on punched tape or a magnetic band, and further processed in data computers as desired.

From the graphs produced or from the indicated average values of microtome cut or other relatively smooth surfaces, the dimensions of anatomic structural details and respective density figures can be derived. Figure 2 shows two styli of a tracer instrument in position on a wood surface.

When measuring cell dimensions the measuring lengths or thicknesses are expressed in microns (μ). For computation of cell-cavity dimensions, certain mathematical model assumptions have to be made to enable translation of length measurements into area values, Stamm (1946) and Suchsland, K. (1957). In Suchsland's

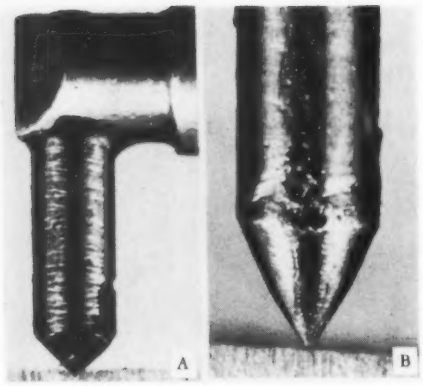

FIGURE 2. *Two styli used in this study. A. pyramidal diamond tip for high resolution. B. Steel cone tip for low resolution* (× 17.5).

study, at the Swedish Forest Products Research Laboratory, it was found that a cross section of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) conformed closely to the mathematical model of rectangular cell cross sections. For cells of circular or polygonal (isodiametric) cross sections, the cell-wall thickness w can also be calculated from:[4]

$$[1] \qquad \rho^2 \pi - \pi \left(\rho - \frac{\overline{w}}{2}\right)^2 = W$$

$$[2] \qquad \frac{\pi \rho^2 r_0}{\gamma} = V$$

$$[3]) \qquad \overline{w} = 2\rho \left(1 - \sqrt{1 - \frac{r_0}{\gamma}}\right)$$

$$\text{and since } \rho = \frac{\overline{L}}{2}$$

$$[4] \qquad \overline{w} = \overline{L} \left(1 - \sqrt{1 - \frac{r_0}{\gamma}}\right)$$

$$[5] \qquad r_0 = \gamma \frac{2\overline{L}\overline{W} - \overline{W}^2}{\overline{L}^2}.$$

The formulas can be expanded to give approximate results for cells of anisodiametric cross section if the averages of the major and minor axes are used.

Figure 3 illustrates schematically the cell-cavity and cell-wall dimensions for measurement. The analysis of graphical representation of the anatomic structure must be in conformity with assumed models, and measurements have to be made consistently and uniformly. This is especially the case with microscopic measurements, where planimetric methods are to be compared with results obtained through tracer instruments. Mork's (1928) definition, although originally intended for spruce, has been used as a standard in our growth ring studies. His definition as applied to Norway spruce (*Picea abies* (L.) Karst.) is as follows: "All tracheids in which the common wall between two cell cavities multiplied by 2 is equal to or larger than the width of the lumen, are considered as summerwood; those in which the value is less than the width of the lumen are considered as springwood" (all measurements made in the radial direction). Figure 3 illustrates this definition.

For the details of automatic integrating

[4]For the definition of terms and symbols, see list preceding the "literature cited" near the end of this article.

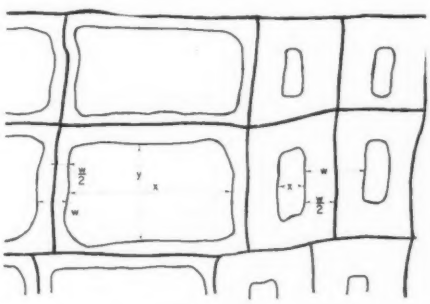

FIGURE 3. *Schematic representation of cell-cavity and cell-wall dimensions for measurement by microscope or tracer instrument. Summerwood: 2 w* $\geqq$ *X. Springwood: 2 w* $<$ *X.*

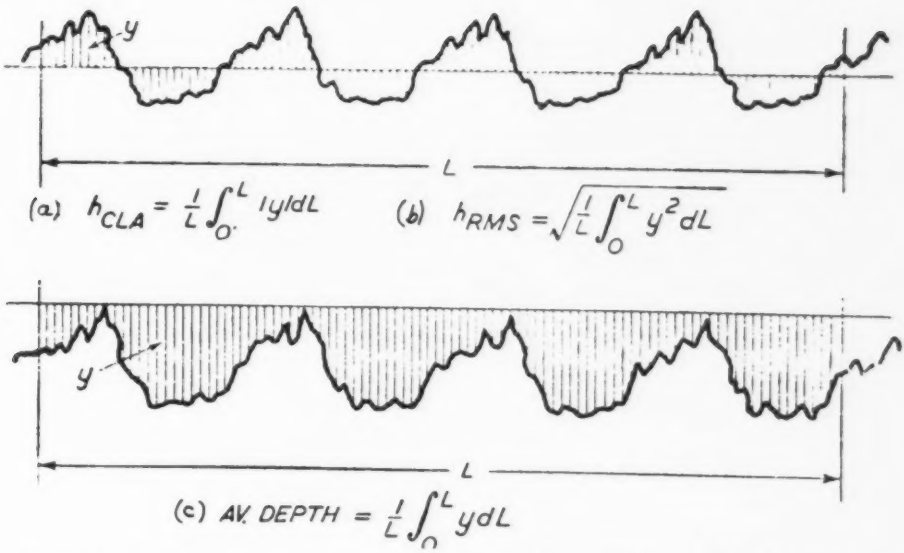

FIGURE 4. *Methods of numerical assessment of average values. C.L.A. and R.M.S. are most commonly used, but crest line average is most suitable for growth ring measurement. (a) Center line average; (b) root mean square; (c) crest line measure.*

and averaging of graphical records, see Marian.[5] Three of the most common methods of numerical assessment are shown in Figure 4. Center line average and root mean square are functions of the height of the graph; therefore, to determine the width of cell cavities, it is necessary to express a relationship between the height and width of the trace. The relationship $x = kT_a \tan \phi$ where k is a constant, ideally equal to 2, was developed (Fig. 5). If ϕ is 45°, as in the case of the instrument used, then tan ϕ becomes 1 and the relationship becomes: $x = 2T_a$.

In other words, twice the tracing depth equals the cell-cavity dimension. This equation is valid only so long as the tracer tip does not "touch bottom," as in the case of the end-grain surfaces, with a stylus of appropriate dimensions. For other grain directions, different relationships are valid but are not considered here.

[5] *Op. cit.*

From Figure 4 it is clear that the "crest line measure" originally proposed by Nicolau (1937) is the most suitable for averaging the graphical record corresponding to $x = 2T_a$. A still more suitable numerical assessment would be a direct averaging of x values, which would give a direct mean value of the cell-cavity dimension.

According to the system of circuits employed, electrical integrating instruments may be constructed to indicate heights on different bases of assessment. A well known proposition in applied mathematics, Fourier's Theorem, shows that the form of any regularly repetitive profile can be expressed as the sum of a series of pure sinusoidal components of appropriate amplitudes, the dominant wavelength being that of the profile, the wavelength of the other components being successive simple fractions thereof, e.g., 1/2, 1/3, 1/4, 1/5.

The operation of such an electrical instrument can be considered as a process of resolving the form of the profile under ex-

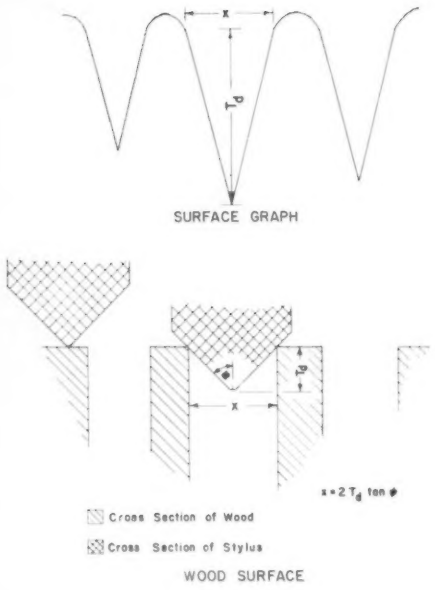

FIGURE 5. *Determination of cell-cavity dimensions and cell-wall thickness from tracing depth measurements showing the point of measurement on a surface graph.*

amination into its sinusoidal components and recombining those components in such a manner as to carry out, automatically, the process of integration necessary to give the average value.

Once the average for x or T_d is derived, the average cell-wall dimension relative to cell-cavity dimension can be computed according to equations [6] and [7]:

$$[6] \qquad L - \Sigma x = \Sigma w$$

$$[7] \qquad \bar{w} = \frac{L - \Sigma x}{n}.$$

If we assume Mork's definition, then:
$2w \geq x$ for summerwood
$2w < x$ for springwood, which can be either derived from the graph or electrically computed.

For consecutive growth ring analysis the following modifications of the instrument should be considered: (a) use of blunter stylus, (b) traversing objects instead of stylus, (c) meter indications and recording of growth ring characteristics according to mathematical definitions such as that of Mork.

Determination of Density from Surface Texture Measurements

Density must be considered as the most important variable in timber physics (Brown *et al.* 1952, Kollmann 1951, Huber 1951, and Smith 1954). A rapid, accurate method based on micro-samples and on concepts different from weight-volume relationships or the maximum moisture content method (Keylwerth 1954, Smith 1955, and Trendelenberg and Mayer-Wegelin 1955) would therefore be useful in many research and practical applications. To date, the only attempted method with this objective is the optical, photoelectric determination of specific gravity according to Müller-Stoll (1948), Kollmann (1951), and Huber (1951). For practical purposes the usefulness of this method is debatable (Kollmann, 1951).

The derivation of density from tracer graphs or integrated averages was attempted in the present study. Preliminary results are given in Tables 1 and 2. The basic idea of the method is to determine on microtome cut surfaces, cell-cavity and cell-wall dimensions by tracer instrument records or indications — in other words, pore volume, P, and cell-wall substance (volume fill-in), F—and to compute these to specific gravity figures with the aid of the Kollmann-Trendelenburg diagram shown in Figure 6.

The validity and accuracy of this method, therefore, depend (among other factors) on the constancy and accuracy of the determination of γ = density of wood substance, but not as in the method of Keylwerth, in which the maximum moisture = u_{max} is determined from weight/volume relationships (Keylwerth, 1946), or as in the optical method of Müller-Stoll (1948).

Keylwerth uses the equation [8] based on the relationships:

$$[8] \qquad R = \frac{W_d}{V_w}$$

$$u_{max} = \frac{W_w - W_d}{W_d} \left[\frac{g}{g} \right]$$

$$u_{max} = \frac{1}{R} - \frac{1}{\gamma} \left[\frac{g}{g} \right]$$

$$R = \frac{1}{u_{max} + 1/\gamma} = \frac{1}{u_{max} + 0.667}.$$

Random Samples for Application of the Method

Consecutive growth ring analysis. For a number of purposes it is necessary to study growth rings laid down over a certain time period, for instance, during the past 10 to 50 or even 100 years. In such cases, it will be necessary either to reset the tracer instrument for sequential measurements or, more simply, to move the samples instead of the tracer stylus as is now done. Details of this arrangement will have to be worked out in connection with the development of adequate data processing and for coding and storing data directly from electrical impulses. A graph for a preliminary and exploratory run with a blunter tip on a transverse surface of Douglas-fir is illustrated in Figure 7.

Relative histometry.[6] In wood anatomy, certain fundamentally important problems, such as the identification of species or the

[6]According to Recker (1949), relative histometry is the quantitative assessment of philogenetically or functionally similar tissues, consisting of identical cell elements, in tissue aggregates.

TABLE 1. Planimetric density determinations.

Test number	Weight of fill-in (mg)	Porosity weight (mg)	Total weight (mg)	Percent fill-in (F)	Percent porosity (P)	Density (r_o)
1R	5.832	1.668	7.500	78	22	0.82
2R	3.272	5.349	8.621	38	62	0.40
3R	6.570	2.033	8.603	76	24	0.80
4R	3.232	4.583	7.815	41	59	0.43

TABLE 2. Surface texture density determinations.

Test number	Sum of radial pore widths (Σx)	Total radial width (L_r)	Total tangential pore width (Σy)	Total tangential width (L_t)	Percent porosity $\frac{\Sigma x \cdot \Sigma y}{L_r \cdot L_t}$ (p%)	Density (r_o)
			Units			
1R	23.3	50.5	38.5	83.2	21.2	0.83
1R′	30.6	75.8	31.4	83.8	15.1	0.90
2R	85.2	110.8	66.1	85.6	59.3	0.43
2R′	105.1	129.2	71.2	84.3	68.3	0.34
3R	36.7	76.6	28.9	91.2	15.0	0.90
3R′	31.7	73.0	37.2	93.1	16.8	0.88
4R	83.8	112.4	62.2	86.3	56.6	0.50
4R′	82.3	120.9	69.9	107.6	45.4	0.57

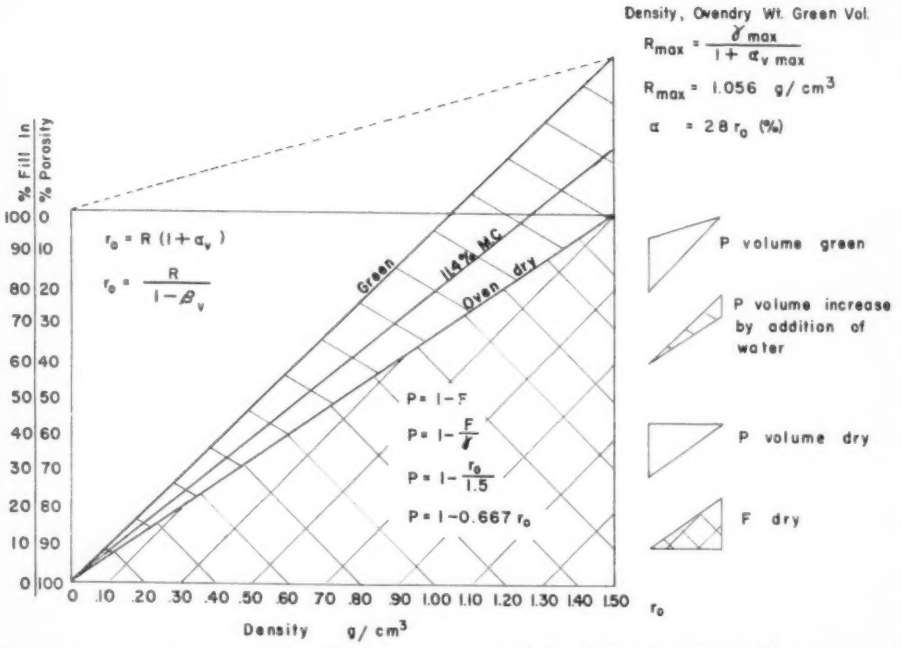

FIGURE 6. *The Kollmann-Trendelenburg diagram used for derivation of specific gravity and density.*

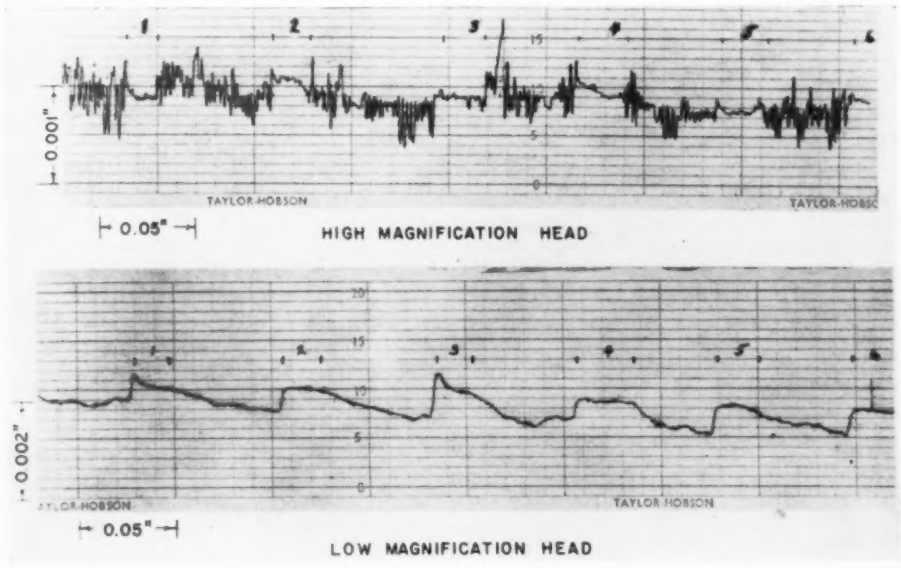

FIGURE 7. *Surface texture graphs showing growth ring measurements. Numbered areas correspond to summerwood.*

relationship between qualitative and quantitative growth increment have to be solved by "relative histometry," the results of which are easily reproducible and amenable to statistical analysis. Moreover, in tree breeding it is quite generally recognized that the selection of optimum individuals not only depends on morphological characteristics but also on the more significant data of wood anatomy and the mechanical and physical properties of the timber (Marquardt 1956, Pryor *et al.* 1956).

So far, two methods have been available: (1) planimetric measurement of highly magnified photomicrographs or projections, and (2) the so-called "planimetric analysis by the linear intersection," called "linear-taxation" in Scandinavian forest mensuration, and originally employed by Yatsenko - Khmelevsky and Bregadze (1939) in Russia. In botany, this method has been extensively used by Huber and Prutz (1938), and quite recently by Liese and Meyer-Unlenried (1957).

The tracer technique potentially provides a rapid method for the quantitative recording of different tissue components in a single graph. A preliminary example is shown in Figure 8. A quantitative evaluation can be carried out according to the same principles described for growth ring analysis. This technique is naturally applicable only to geometrically and mathematically definable features.

Experimental Methods and Data

Growth ring analysis. Growth ring measurements such as are needed for springwood-summerwood percentages, rings per inch, average annual increment, etc., can be determined from the recorded graph (Fig. 7) or by integrated values.

The accuracy of the instrument is calibrated by means of a test plate,[7] the graph magnification by the use of lines of known depth, and the center line average by a grid system of etched lines with a known C.L.A. It is possible to adjust the C.L.A. meter to within ± 0.2 micro-inch C.L.A. of the standard value. A further calibration of the instrument was carried out with the aid of special wire gauzes used as specimen supports in electron microscopy (Fig. 9). The measurements on the surface texture graphs were found to correspond exactly to those made under a microscope, i.e., 0.0021 inch.

The annual increment, or rings-per-inch determination, is made by measuring the width of the growth ring. This can be done either manually or by automatic integration. An example of manual ring measurements found 3.8 rings per inch (Fig. 7).

The measurement of springwood-summerwood percentages is complicated by the

[7]Talysurf test plates were provided by the National Physical Laboratory, Teddington, Middlesex, England.

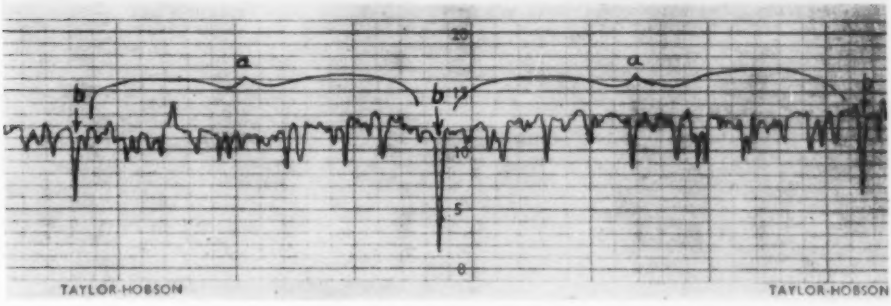

FIGURE 8. *Tracer graph on Douglas-fir showing:* (*a*) *tracheids,* (*b*) *ray cells.*

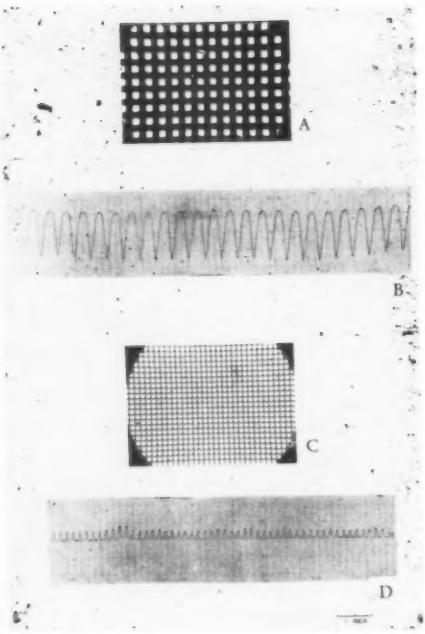

FIGURE 9. *Calibration of the instrument by means of wire mesh grids used as specimen supports in electron microscopy. A. Wire mesh, 200 per inch (× 15.4). B. Talysurf graph, wire mesh, 200 per inch, (× 20). C. Wire mesh, 500 per inch (× 15.1). D. Talysurf graph, wire mesh, 500 per inch (× 20).*

necessity of determining the point within the annual ring where the springwood ends and the summerwood begins. This involves defining springwood and summerwood. We have used the definition proposed by Mork (1928) (Fig. 3). The measurements are made on a projected image of a surface graph. The cell cavity border was determined by the point of inflection of the curve (Fig. 5). The calculations for the examples of Douglas-fir shown in Figure 7 are:

Total ring width = 19.0 units
Springwood width = 14.5 units
Summerwood width = 4.5 units
Springwood percentage = 76
Summerwood percentage = 24.

The measurements can be simplified by the use of automatic integration of the type discussed later.

Porosity and density determinations. In the process of developing a method of density and porosity determinations by surface texture measurements, it was necessary to compare the results of the tracer method with several known methods. The methods used were the weight-volume, maximum-moisture, and planimetric. Specimens of Douglas-fir for the tests were selected to assure the least possible variation in the material (Fig. 10).

The values of weight-volume and maximum-moisture tests are the averages of two tests in each ring. They were calculated on the basis of green volume and oven-dry weight, and then converted to oven-dry volume, oven-dry weight by the formula: $r_o = R\ (1 + \alpha_v)$ where $\alpha_v = 0.28\ r_o$ (Keylwerth, 1954).

To determine the density by planimetric methods, the sections were mounted in water, in green condition, and a photomicrograph of each area was taken. The areas were chosen to correspond as nearly as possible to the test blanks used in the weight - volume and maximum - moisture

FIGURE 10. *Method of selection of test specimens. RT = block for surface graphs. RS =section for planimetric method. RW = blocks for weight-volume method.*

tests. The cell-cavity areas were cut from the photographic print and weighed. This weight divided by the total weight of the cell-wall and cavity area gave the percentage of pore area, which is equivalent to percentage of pore volume, that is, percentage porosity. The porosity figure was then converted to density based on oven-dry volume and oven-dry weight, by the Kollmann-Trendelenburg graph (Fig 6, Table 1).

From surface texture measurements and cell-wall size the percentage porosity can be calculated as in the planimetric tests, and the density can be found again by referring to the Kollmann-Trendelenburg graph.

To test the validity of the function $x = 2T_d \tan \phi$, wire gauzes (Fig. 9) were used. The actual measurements of the gauze under the microscope were: wire = 0.0018 inch, mesh = 0.0031 inch, total = 0.0049 inch. The width x on the tracer graph was found by actual measurement. The point used for measurement was the point of inflection of the curve (that is, the point at which the curve of the peak ended). The depth, T_d, was taken as the distance from that point to the intersection of the slopes forming the valley (Fig. 5). The measurements thus found were: $x = 0.0031$ inch (this corresponds to the measured value under the microscope), $T_d = 0.0013$ inch, $2T_d = 0.0026$ inch. This would make $x \approx 2.38T_d$.

The relationship between height and width of trace was checked on wood several times. The results of a test on springwood found $\bar{x} = 42.8$, $\bar{T} = 13.5$, which means that $x = 3.17\ T_d$.

Until a clear picture of these height-width relationships is available, it is necessary to use direct measurement for density determination. The Douglas-fir block used for the study was first saturated with water, and two tangential and two radial traces were run over each test area. The block was then dried to 11.4 percent moisture content by solvent (acetone) extraction to avoid, as much as possible, distortion or deformation through shrinkage on drying, and the graphs were then repeated to determine the effect of change in moisture content on the values obtained. The graphs were photographed and projected to give sufficient magnification for measurement. The pore dimensions x and y and trace lengths L_t and L_r were measured for 40 cells, n = 40. The formula

$$P = \frac{\Sigma x \cdot \Sigma y}{L_t \cdot L_r} \qquad [9]$$

gives the percentage porosity. This calculation is based on the assumption that the cells approximate a rectangle. The percentage of porosity can then be converted to density by the Kollmann-Trendelenburg graph. Results are given in Table 2. Table 3 shows a comparison of the three methods.

If an elliptical cell-cavity model is assumed, the percentage porosity for one example (1R) is 16.8 instead of 21.2, and the density is 0.89 as compared with 0.83.

If formula [5] is used to calculate the density, the results are found to correspond to the values of the Kollmann-Trendelenburg graph. For example, the density of 1R by this method is 0.85 compared to 0.83 by the Kollmann-Trendelenburg graph.[8]

Discussion

The calibration (agreement between direct microscopic measurement and tracer data) can be considered satisfactory. It has to be borne in mind that the wire gauze is not an ideal test object; the cross section of the wire filaments is not exactly circular, the meshes are not exactly geometrically correct, and the pyramid-shaped stylus may also contribute to the discrepancy between the geometrically postulated relationship $x = 2T_d$ and the observational data. The relationship $x = 2.38\ T_d$ is considered acceptable until a more suitable test object can be found.

[8] 1.077, the density of solid wood substance based on green volume, was used for γ (Brown *et al.* 1952).

TABLE 3. Comparison of weight-volume, planimetric, and surface-texture density values.[1]

Specimen number	Density Weight-volume (av. of two tests)	Density by planimetric method	Density by surface texture[2] (av. of two tests)	Density surface texture[3]
1R	0.81	0.82	0.86	0.98
2R	0.29	0.40	0.39	0.69
3R	0.77	0.80	0.89	1.03
4R	0.27	0.43	0.53	0.61

[1]All tests are given on the basis of oven-dry weight and volume.
[2]Test taken at maximum moisture content.
[3]Test taken at 11.4 percent moisture content.

The automatically integrated C.L.A. index values obtained on etched-glass test plates were in perfect agreement with postulated values. The automatic integration of the test plates supplied by the National Physical Laboratory, Teddington, England, shows perfect agreement between graphically and automatically integrated values of the graphs. The graph made by tracing of the wire gauze gave an instrumentally integrated value of C.L.A. = 200+, and graphically, C.L.A. = 468; in other words, the wire gauze is outside the range of this instrument's automatic integration.

The C.L.A. index value was chosen for surface texture studies on wood because it is one of the commonly used values in the United States and England. After it was discovered that this tracer instrument could be used for representing anatomic details graphically, a mathematical assessment became desirable. The C.L.A. unfortunately was the least suited index value since it has no direct geometrical meaning as does the "peak-to-valley" or "crest line average" value. We therefore resorted to graphical integration. From the relationship $x = 2T_a$ we chose to determine x rather than T_a because it appeared that imperfections of the cut surfaces were of less influence, and because of the discrepancy observed in calibration with the aid of the wire gauze. A similar but larger discrepancy was observed on wood, which will be investigated further to determine its causes and magnitude. Until this is accomplished, it is thought preferable to determine cell-cavity dimension $\bar{x}$ from the magnified graphs directly. Graphical integration naturally means, to some extent, dependence on individual, personal data collecting; thus the results are influenced by conscious or subconscious human factors. These would be entirely eliminated by automatic integration.

The objective of this investigation was to establish fundamental principles. The real statistical analysis of experimental, large-scale data has to be postponed until the instrumental problems of automatic integration can be solved. *However, it appears to be established that it is possible to resolve anatomic details by means of tracer instruments in which displacements of the stylus are transformed into electrical impulses in a mathematically assessable relation.* The resolution and magnification of the tracer instrument compare favorably with the light microscope and, in some respects, can be made to reach the resolution of the electron microscope, with magnification of $1 \times 50{,}000$ or $1 \times 100{,}000$.

The determination of the springwood-summerwood border line is a relatively simple task. It is possible to reduce the power of resolution by using a blunter tip than the diamond stylus, as shown by a preliminary radial run on a sanded, transverse surface of Douglas-fir (Fig. 7). This method again opens a path for automatic

recording of growth ring data in a consecutive system. The quantitative derivation of latewood percentage averages ($\bar{s}$) on the basis of Mork's definition will be attempted when automatic integration is available.

The values for maximum moisture content $\alpha_v = 28r_o$ [%] is an assumed approximation. Replacement by actual experimental data from Douglas-fir probably will bring the figures closer together. It should be remembered that the density figures obtained according to various methods (oven drying, solvent extraction, etc.) also vary considerably. The basically similar methods of planimetric and surface texture measurements are in fairly good agreement. Any statistically established differences from density figures obtained by existing conventional methods would certainly be interesting new knowledge.

Conclusions

The data presented in Tables 1 to 3 are too scanty to permit drawing definite conclusions beyond the statement that the feasibility of the method as a rapid, simple, micro- and semi-nondestructive test can be considered established. The limits of accuracy will be found when automatic averaging of measurements becomes possible. The advantage of samples 0.01 to 0.1-inch long (linear tracks) is obvious. That density is derived from direct porosity data and not from weight-volume relationships is a definite advantage in the study of wood moisture conditions or processes.

The data obtained can be automatically averaged (integrated), thereby making possible the mass processing of recorded data. The method would eliminate the human element from observations caused by the individual equation of the operator, as errors caused by fatigue, etc. The mathematical assessment is truly objective and independent of the skill of the individual operator. The rapidity of data collection would be limited only by the optimum traversing speed and the rate of feeding samples into the instrument. Further experimental work is necessary to solve problems of instrumentation and establish the applicability of the methods presented to problems of forest botany, genetics, timber physics, and wood technology.

Some of the immediate applications can be foreseen in the determination of density and of latewood percentage for Ylinen's equations (1942, 1956), and in swelling and shrinkage of coefficients.

Results obtained suggest a certain elastic deformation of the cell-wall substance under tracing pressure. Potentially this indicates that it would be possible to measure deformation under variable pressure[9] — in other words, to determine the elastic constants of the cell-wall substance by the empirical formula

$$[10] \qquad \sigma_{max} = \sqrt[3]{\frac{0.059pE^2}{\left(\frac{d}{2}\right)^2}}$$

for the deformation under the load of a spherical tip (Hertz, 1895).

The Future of the New Method

It should be remembered that the instrument used is a standard type, designed to measure surface texture in metals, and as such, is not ideally suited to the solution of problems outlined in the paper.

The stylus is a pyramid-shaped diamond with a tip of 2.5μ diameter and a tracing pressure of approximately 10 mg = 0.0004 ounce. The scale of magnification is 1 × 20 or 1 × 100 on the horizontal, and 1 × 1,000; 1 × 2,000; 1 × 5,000; 1 × 10,000; and 1 × 50,000 in the vertical direction. Automatic integration is indicated in C.L.A. index values.

An ideal instrument should probably have the following characteristics: (1) cone shaped stylus of some inexpensive material, as quartz, sapphire, or tool steel and a stylus tip of approximately 10 to 15μ diam-

[9]Compare the monograph by A. Frey Wyssling, "Deformation and flow in biological systems. Deformation of plant cells." (Wyssling, 1952).

eter with variable tracing pressure, possibly less than 10 mg; (2) a micrometrically adjustable specimen stage that would move under a stationary stylus at a speed of 0.05 inch per second or more; (3) magnifications of about 1 × 20; 1 × 100; and 1 × 1,000 in the horizontal and 1 × 1,000 in the vertical direction.

Automatic integration of the border line of the growth ring should be indicated according to mathematical definitions of ratios of cell wall to cell cavity, for instance, as given by Mork (1928) and automatic indication of cell-cavity dimensions according to variable maximum and minimum rules and averaging in crest line values by automatic integration or direct averaging of cell-cavity dimensions ($\bar{x}$ values).

The specimen might be an increment core or a block of wood and would only be limited in size by the design of the specimen stage and convenience of preparation. The preparation would consist of microtome planing of the surface which a properly trained and equipped worker could do rapidly. A sample of any moisture content could be used but that of green wood would be most convenient.

The operation of the instrument would consist of adjusting the specimen under the stylus, automatically advancing the stage and specimen past the stylus, reading the data, and recording it. At the rate of traverse suggested, this operation could be accomplished, for a 3-inch specimen, in about 2 minutes.

Experience gained in past growth ring research in the United States, Canada, the Scandinavian countries, and continental Europe seems to indicate that it is advantageous to concentrate research activities at one center where all the necessary facilities are available, including special tracer equipment and statistical resources for computation of the voluminous observational data. The observational material is singularly suited for this type of organization since the most frequently used material—increment cores—could easily be mailed to such a center for evaluation.

The creation of a center for growth ring research with a wide scope in forestry—based on this new method as a potential tool — could revitalize such studies in the United States and intensify them elsewhere in forestry laboratories.

Summary

A brief history is presented of the development of techniques and methods for measuring growth rings.

A new technique based on graphical records obtained with a stylus tracer-type electronic instrument is described. Essentially, this instrument transforms mechanical displacement of a stylus into electrical impulses, determined by the electrical characteristics of the instrument. Averaging of the graphically obtained data can be performed by automatic integration in any conventional system of quantitative assessment—C.L.A., R.M.S., and peak-to-valley or crest line values. Cell-cavity and cell-wall dimensions, springwood and summerwood distribution within growth rings, porosity, cell-wall substance and density can be derived either by simple measurement and averaging (graphical integration) or by automatic integration by the instrument. This method eliminates the human element from observations. The mathematical assessment is truly objective and independent of the individual operator. The rapidity of data collection would be limited only by the speed at which samples can be fed into the instrument.

Density determinations are compared with conventional methods based on weight-volume relationships, maximum moisture, and planimetric methods. Preliminary results indicate fairly good agreement among different methods. The advantages of this method—using sampling length 0.01 to 0.1 inch for tracing—and its nondestructive nature are emphasized especially for the problems of timber physics.

Application of the method for consecutive growth ring measurements is discussed and demonstrated.

Discussed also are a few applications of

the new method to some problems of timber physics: determination of density for Ylinen's equations, swelling and shrinkage coefficients, relative histometry, and the derivation of the elastic constants of the cell-wall substance.

The applications of the new method to problems of forest botany, genetics, and mensuration are briefly mentioned. The principles for the construction of a specialized instrument built for forestry applications are stated and discussed.

List of Terms and Symbols Used

x, y Cell-cavity dimension according to Figure 2.

$\bar{x}, \bar{y}$ Mean cell-cavity dimension (average).

w Common cell-wall thickness (between 2 cells) $= \dfrac{L - \Sigma x}{n}$.

$\bar{w}$ Mean common cell-wall thickness (average).

T_d Tracing depth according to Figure 3.

2ϕ Angle formed by planes of stylus-tip pyramid.

L Length of sample track used for trace (actual measurements).

$\bar{L}$ Average length of cells (L/n).

n Number of cells on sample track.

r Density of wood.

r_o Density of wood, weight oven-dry, volume oven-dry.

r_u Density of wood, weight oven-dry, volume at (u) moisture content.

R Density of wood, weight oven-dry, volume green.

R_{max} Density of wood, weight oven-dry, volume at maximum moisture content.

γ (gamma) Density of wood substance ≈ 1.5.

ρ (rho) Circular cell outside radius.

W Weight of unit length of cell.

W_d Weight of unit length of cell oven-dry.

W_w Weight of unit length of cell wet.

V Proportional solid volume corresponding to W.

V_w Proportional solid volume corresponding to W_w.

P Porosity, area or volume porosity according to Figure 8.

F Fill-in, area or volume of wood substance.

α_v Coefficient of volume swelling.

β_v Coefficient of volume shrinkage.

$\alpha_{v_{max}}$ Coefficient of maximum volume swelling.

u Moisture content in percent.

u_{max} Maximum moisture content in percent.

s Latewood percentage.

h_{CLA} Center line average index value $= \dfrac{1}{L}\int_0^L |y| \, dL$

h_{RMS} Root mean square index value $= \sqrt{\dfrac{1}{L}\int_0^L y^2 \, dL}$

h_{crest} Crest line depth, crest line average depth index value $\dfrac{1}{L}\int_0^L y \, dL$

$x = 2T_d = \dfrac{L}{2}\int_0^L y \, dL$ according to Figure 7 and Figure 3.

σ_{max} (sigma) Maximum deformation under given tracing pressure p of the cell-wall.

p Tracing pressure in Hertz's equation.

d Diameter of spherical tip of the tracer stylus.

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Supplement July 1958-June 1959, Including Additions for 1900-June 1958

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CONSTANCE BATTAILE

Subject Index by
RAY A. YODER
WILLIAM I. WEST

A LIST of forestry theses for January 1956-June 1958 was published in *Forest Science*, Volume 5, Number 3, September, 1959. Information is given there on availability of earlier lists and lists covering related subjects.

The list of forestry theses for this supplement presented alphabetically by institutions follows.

Alabama Polytechnic Institute

1956

1. Moore, William Holtam. Effects of certain prescribed fire treatments on the distribution of some herbaceous quail foods in loblolly-shortleaf pine communities of the Alabama upper coastal plain.

1957

2. Hopper, Bruce Evan. Nematodes in the soils of southern forest nurseries.

1958

3. Nichols, Neil Grady. Some factors affecting lateral root development of longleaf pine in southwest Alabama.

1959

4. Padgette, William Hanson. Soil fungi associated with damping-off and root rot diseases of pine seedlings in selected Alabama forest nurseries.

University of California

1958

5. Griffin, James Richard. A study of the distribution of *Pinus ponderosa* Laws. and *Pinus attenuata* Lemm. on sandy soils in Santa Cruz County.
6. Hickey, Wayne Clayborne. Yield prediction equations for crested wheat grass grown under varying climate and varying intensity of use.
7. *Kuijt, Job. Morphological aspects of parasitism in the dwarf mistletoes (*Arceuthobium*).
8. *Wagle, Robert Fay. Early growth variation in bitterbrush and its relation to environment.

1959

9. Libby, William John. Rooting responses of eastern white pine (*Pinus strobus* L.) to application of lanolin and kinetin.
10. McDonald, John Bruce. An ecological study of Monterey pine in Monterey County, California.

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*An asterisk before a thesis indicates a doctoral dissertation.

Mrs. Osborn and Mrs. Battaile are librarians at Oregon State College, Corvallis. Professors Yoder and West are with the School of Forestry at the same institution.

11. Plumb, Timothy Roy. Determining the crown closures of forest stands from aerial photographs.
12. Riberolles, Jean Pierre Victor de. The influence of the surface texture on strength of butt-end glued wood.
13. Schlappi, Elizabeth Roe. Saving the redwoods.
14. Smith, Leslie V. Diurnal variations of the sugar content of sugar pine (*Pinus lambertiana* Dougl.) foliage.

Colorado State University

1958

15. Alexander, Robert Ritchie. Thinning lodgepole pine in the central Rocky Mountains.
16. Bowen, Anne La Bastille. Ecological analysis of mule deer winter range, Cache La Poudre Canyon, Colorado.
17. Dietz, Donald R. Seasonal variation in the nutritive content of five southwestern Colorado deer browse species.
18. Garrison, Verne Lee. Primary problems involved in marketing privately-owned stumpage in west-central Colorado.
19. Hart, Ray D. Evaluation of deer pellet group census method, Black Hills, South Dakota.
20. Henley, John Wyatt. A log quality grading system for ponderosa pine near Flagstaff, Arizona.
21. Hughes, Jay Melvin. Price and prejudice in the marketing of Colorado lumber.
22. Mustard, Eldie W., Jr. Browse differences in experimental pastures under controlled stocking with cattle, sheep, and mule deer in northwest Colorado.
23. Phillips, David Congdon. The use of a lumber tally as a system of scaling.
24. Rate, Henry Adams. Effects of moisture and shade upon germination and survival of ponderosa pine in the Southwest.

1959

25. Bond, Henry E. Revegetation and disintegration of pocket gopher mounds on Black Mesa, Colorado.
26. Owusu-Afriyie, Abraham Kwabana. Some problems encountered in forest management in Ghana.
27. Schuster, Joseph L. The relation of root development of native plants to grazing intensity of ponderosa pine ranges.
28. Simon, Charles Lee. The effect of cold storage and grading on coniferous nursery stock survival.
29. Van Haverbeke, David Francis. Root development of ponderosa pine seedlings in the Black Hills.

Duke University

1959

30. *Applequist, Martin Benjamin. A study of soil and site factors affecting the growth and development of swamp blackgum and tupelogum stands in southeastern Georgia.
31. Blackstock, Clarence Ernest, Jr. A survey analysis of input-output factors in the management of southern pine.
32. Bower, David Roy. Volume of pine sawlogs as predicted by volume-weight relationships.
33. *Carter, Mason Carlton. The phytocidal action of 3-amino-1,2,4-triazole on honeysuckle (*Lonicera japonica*).
34. Moehring, David Marion. Some observations on the distribution of pine roots in certain soils of southeastern Arkansas.

University of Georgia

1959

35. Fowler, Oscar Selman. The relative accuracy of 5, 10, 20, and 40 percent cruises with ½, 1, and 2 chain strips on 50 and 100 acres.
36. Shelhorse, Albert W., Jr. Variation in slash pine plantations located in the middle coastal plain of southern Georgia.

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37. *Kaufman, David. Protoplasmic streaming in pine cambium.
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40. *Thomas, Joab Langston. The Cyrillaceae.

41. *Whitehead, Donald Reed. Pollen diagrams from the western Carolina piedmont.

University of Idaho

1957

42. Oien, Waine E. A pre-logging inventory of four trout streams in northern Idaho.

1958

43. Bachman, Roger Werner. The ecology of four north Idaho trout streams with reference to the influence of forest road construction.
44. Nickle, William Robert. Nematodes associated with the rootlets of western white pine in northern Idaho.

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46. Hill, Robert Bailey. A study of leader elongation in western white pine.
47. Skovlin, Jon Matthew. A study of the relative utilization of important forage plants on summer cattle range in the Blue Mountains.

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49. Henderson, Jerald Milton. Hardened nail in a single nail laterally loaded wood joint.
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1959

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53. MacPeak, Malcolm D. Some factors affecting the specific gravity of plantation grown red pine.

Louisiana State University

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54. Ferrill, Mitchell Davis. Growth of American sycamore.

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55. Branton, David William. The effects of repellents and storage after treatment on germination of loblolly and longleaf pine seed.
56. Dalhoff, Frank B., Jr. Lamination of preservatively treated southern pine.
57. Linnartz, Norwin Eugene. Estimation of site quality for southern pines through measurement of certain soil and topographic features.

University of Maine

1958

58. Alden, Howard R. An ecological analysis of spruce-fir stands in the Kennebec River Valley, Maine, ten years since clear-cutting.
59. Czapowskyz, Miroslaw Miro. An investigation of the effect of certain soil and stand variables upon the height and basal area growth of Norway spruce in central and southwestern Maine.

1959

60. Alkon, Philip U. A study of nutritional and palatability values of hardwood slash as winter deer food.
61. Robinson, William L. A study of shelter requirements of penned whitetailed deer.

University of Massachusetts

1959

62. Gehling, Raymond L., Jr. Evaluation of abandoned fields from aerial photographs as cottontail rabbit habitat.
63. Moore, Dwight David. Ecological changes and wildlife uses in impounded areas with emphasis on flooded forest swamps.

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64. *Sheneman, Jack M. Microbial activity in maple tree tapholes and its relation to sap yields.

1958

65.* Coltharp, George B. Some effects of a commercial-type clear-cut on soil and

water relations on a small wooded watershed.

66. *Huey, Ben M. Selected economic alternatives for logging lodgepole pine.
67. Niloofari, Parviz. Macroscopic identification of most important Iranian timber species and wood utilization in Iran.
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69. Snook, Frederick. A study of some variables in an extruded particle board process.
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71. Bey, Calvin F. The five-year intercept method of site index determination for red pine.
72. Crews, Donald L. The effect of dowel diameter and hole depth on dowel joint strength.
73. Falasky, Emil V. Residual stand growth in hardwood selection cuttings on the Fred Russ Forest.
74. Luebs, Donald F. Nail-glued wood-plywood I-beams for residential construction.
75. Younger, John O. A critical analysis of a test method for multiwall bags.

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77. Eckhart, Michael Dean. Forestry education in the school; activities which can be utilized to stress forestry concepts.
78. *Howenstine, William L. An evaluation of conservation education in relation to the total program in eight school camps.
79. *Messner, Clarence J. The development of try-out of a set of criteria for the evaluation and improvement of a conservation education program in an elementary school.
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81. Thompson, Walter J. Workmen's compensation in the forest industries.

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82. Adler, Max Eugene. Browse utilization by deer on the George Reserve, Michigan.
83. *Barnes, Burton V. Natural variation in clonal development of *Populus tremuloides* and *P. grandidentata* in northern Lower Michigan.
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85. *Buckman, Robert E. The growth and yield of red pine in Minnesota.
86. Campbell, Robert W. The development of environmental resistance tables for gypsy moth (*Porthetria dispar* L.).
87. Chilman, Kenneth C. A critique of inventory and management plan development in the central Sierras.
88. Foulger, Albert Neil. Some effects of partial cutting on an upland hardwood stand in southern Illinois.
89. *Harrison, Robert P. The insects and diseases of aspen.
90. Henning, Daniel H. Integrating conservation into the naturalist interpretive program of Rocky Mountain National Park and Shadow Mountain National Recreation Area.
91. Hill, Lawrence W. Influence of the establishment and development of a plantation upon some precipitation and runoff relationships on a small watershed in southeastern Ohio.
92. *Kakli, Mohammad S. Some biological aspects of pure and mixed coniferous plantations in Lower Michigan.
93. Martin, Robert E. Stem characteristics affecting tree resistance to fire damage: a problem analysis.
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95. *Peterson, Roger S. Pine gall rust in the Rocky Mountains.
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104. Clausen, Knud E. The natural hybrid of paper birch and bog birch in Minnesota.

105. Waring, Richard H. Some characteristics of the upland forest types in the rock outcrop area of northeastern Minnesota.

Montana State University

1958

106. Addor, Eugene E. The wind-pollinated plants of the Missoula Valley, Montana, with special reference to the flowering seasons.

107. Blakely, Lawrence Mace. Some preliminary studies on the in vitro cultivation of *Pseudotsuga menziesii* callus and the dwarf mistletoe (*Arceuthobium douglasii*).

108. Mitchell, William Warren. An ecological study of the grasslands in the region of Missoula, Montana.

109. Pase, Charles Pierce. An ecological study of sagebrush (*Artemisia tridentata* Nutt.) in western Montana.

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State University of New York College of Forestry, Syracuse

1959

111. Anderson, William Sherwood, Jr. An ecological survey of the birds on the Tully Forest.

112. Armstrong, George R. Economic development in the lumber and plywood industries of western North America: a study in forecasting methods.

113. Ashley, Arthur Nelson. Forest land values in the organized camp.

114. Brock, Robert H., Jr. Photographic coordinate measurement errors and their effect on determination of tilt and resection.

115. *Brody, Harry. Studies in anionic polymerization.

116. *Carrock, Frederick Elias. Methyl affinities of vinyl monomers.

117. Carvalho, José da Silva. Polymerization of levoglucosan.

118. Chaudhari, Narayan Rango. Reversion of induced polyploids.

119. Christiansen, Neils B. An economic comparison of chemical debarking with sap peeling and drum debarking.

120. Day, William Louis. High-temperature kiln drying of hard maple.

121. DeCoste, John Harrison. The relationship of mammals to secondary succession on the Tully Forest.

122. *Dence, Carlton Wilford. The mechanism of the acidic chlorination of softwood lignin.

123. Felton, Kenneth C. Regeneration in certain young conifer plantations in New York State.

124. Garlock, Royal Charles II. Wood preservation: its uses and acceptance in residential construction within New York State.

125. Geacintov, Nicholas E. Grafting onto cellulose using low energy irradiation.

126. *Gleason, Edward H., Jr. Oxidation and grafting of benzyl and ethyl cellulose.

127. Hardjodarsono, Mohammad Sunarjo. The interaction of hypochlorite and white birch wood meal.

128. *Hartenstein, Roy Charles. The effects

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129. Hazard, Sherrill John, Jr. Wet strength development of urea formaldehyde treated papers.

130. Heyse, William Theodore. The mechanical properties of latex treated paper.

131. *Hopkins, Frederick Sherman, Jr. Methodology for the economic analysis of pruning alternatives developed with reference to eastern white pine.

132. Hou, James Cheng-ming. Studies on the mechanism of wet strength development in paper.

133. Kesting, Robert Emil. Studies in chlorophyll-sensitized photoreduction of dye substrates.

134. Klaiber, Harold Milton. A statistical evaluation of predictors of academic success at State University of New York College of Forestry.

135. Koenigs, Jerome W. Fungi associated with diseased red pine roots from plantations in the central New York area, with observations on their pathological significance.

136. Kolhonen, Jukka Antero. Identification and evaluation of factors affecting Finnish newsprint exports from 1927 to 1957.

137. Kutscha, Dieter Franz August. Ultrasonic properties of polymer solutions.

138. Kyi, Soe. The effect of cutting temperatures of yellow birch veneer bolts on plywood shear strength.

139. Lane, Leighton Ernest. Historical study of the formation and development of small woodlots in the Northeast.

140. Lantican, Domingo Manzo. The effect of high temperature kiln drying on some of the physical properties of hard maple.

141. MacTavish, John S. Forest fire damage appraisal.

142. *Marder, Herman Lowell. Studies in copolymer structure.

143. Miller, Roswell K. A survey of landowner cooperation in conservation programs in New York State.

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145. Nelson, Andrew P. A structural and physiognomic description of tropical vegetation.

146. *Noskowiak, Arthur F. Spiral grain patterns in red pine and relationship of age and radial growth rate to change of grain angle.

147. Nyland, Ralph Daniel. Some aspects of forest influences upon air temperature, soil moisture, and soil temperature.

148. *Patric, Jeanne Broley. A system for the classification and cataloging of the literature of the Roosevelt Wildlife Memorial Library.

149. Perkins, Richard Wilson, Jr. An evaluation of the feasibility of employing a face bevel on large-diameter insert-tooth ripsaws.

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